PARASITOLOGY

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PARASITOLOGY

(Founded by G. H. F. Nuttall, F.R.S.)

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VOLUME XXXI APRIL 1939 No. 1

SOME MYXOSPORIDIA FOUND IN CERTAIN FRESH-WATER FISHES IN QUEBEC PROVINCE, CANADA[1]

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(With Plates I–X)

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[1] It is with the deepest regret that we have to state that the senior author, Prof. H. B. Fantham, passed away from septicaemia before the draft of this paper was in its final form. The privilege has been left for us, his fellow research partners, to complete for publication the paper on which he was working the day he died, and which owes so much to his wide knowledge and great experience. A. P. and L. R. R.

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Introduction

The Province of Quebec affords a most interesting field for workers on the fauna and animal ecology of fresh waters. Apart from the great St Lawrence River itself, there are its numerous large tributaries and their still more numerous contributory streams and brooks, so that the country is a network of fresh running waters. In addition, in the Laurentian Mountains, there is a very large number of lakes, and publications show that 30,000 of these are known from aerial surveys. There are also many large and small ponds, permanent and temporary, and bogs and marshes. All harbour aquatic fauna of considerable interest, but the field is practically untouched and its scope is enormous. The Government of the Province of Quebec has shown its interest by developing fish hatcheries for the hatching and distribution of young salmon, trout and bass to suitable waters. Some surveys of a few rivers and lakes for ascertaining their suitability for stocking with these game fish have been made, but the work, having this end in view, has resolved itself largely into determinations of the areas and depths of the waters and a few physical constants of importance such as temperature, suitable for the maintenance of fish. Detailed surveys of the animal populations in the zoological sense have not been made.

It seems highly desirable that exact knowledge should be obtained of the fresh-water animal resources of this great Province, and a beginning in this direction has been made by detailed surveys by some members of the Department of Zoology at McGill University, of certain lakes, ponds and streams. Also, one of us (L. R. R.) for several years has been examining a number of streams and rivers of south-eastern Quebec for the non-game fishes and determining the species present. The other authors (H. B. F. and A. P.) have made ecological surveys of a very few ponds, lakes and streams. However, in the course of all these investigations, smaller non-game fishes, such as suckers, shiners and minnows, and a few game fish in the form of trout, salmon and muskellunge, have been found infected with various Protozoa, Trematoda, Cestoda and Nematoda. As a number of myxosporidian infections have been gradually accumulated, we have pooled our resources and propose to deal with

each type of infection with these parasites separately. A few additional parasites have been obtained from fish bought in local shops.

The present paper deals with some Myxosporidia found in the tissues and abdominal cavities of various fresh-water fishes, protozoal parasites of the gall bladder and of the urinary bladder and those of certain marine fishes being reserved for a future communication.

THE COLLECTING SITES

The waters of the southerly part of the Province of Quebec tributary to the St Lawrence River are divisible into three regions on the basis of faunal distribution. These are the faunistically rich waters of the St Lawrence River Valley, and the comparatively faunistically poor waters of the Laurentian and the Appalachian highlands. Many fishes common in the waters of the valley fail to penetrate far into the mountainous regions.

A large proportion of the fish infected with Myxosporidia herein described was collected personally from waters in the Appalachian area and the infected fish are common to both the St Lawrence River and the Appalachian region. In the Appalachian region there are seven watersheds. The most westerly system is the Pike River, which, with the Missisquoi system, drains into Lake Champlain, and via the Richelieu River enters the St Lawrence. The remaining systems, the Yamaska, St Francis, Nicolet, Becancoeur and Chaudière, which is the most easterly of them, enter the St Lawrence directly, after crossing the broad, flat plain of the St Lawrence Valley. No infected fish have been recorded by us from the Chaudière system, where only highland waters have been examined. The Becancoeur system yielded one infection, in *Poecilichthys exilis*, a species relatively rare in the Appalachian waters. The richest collections of parasitized fish were made in the waters of the Nicolet system at the transitional level between purely highland and lowland conditions, where the river passes from the rough country of the mountains out on to the edge of the St Lawrence Valley plains. At the lower ends of small brooks in sections of the lowland type with slow-running water and meandering courses, the percentage of myxosporidian infection is comparatively high, especially in the case of *Notropis cornutus*, which is very common in such situations. Many of these small brooks and streams, e.g. Francoeur Brook, near St Clothilde, Rivière des Rosières, Rivière des Pins, have yielded heavily infected fish, though the higher levels of the rivers mentioned were uninfected. Similarly, infected fish have been found in the St Francis system in the lowland section of brooks entering the main stream at the transitional level or below it, such as the Black River and the Ulverton River. Infected *N. cornutus* taken near Scotstown forms the most highland of the records of myxosporidian infection from this system, and even they were taken from the lowland reach of a brook above a millpond.

The St Lawrence River itself has not been much examined, but infected *Esox maskinongy*, the muskellunge, has been found in Lake St Louis, an expansion of the river, and *Moxostoma aureolum* at Boucherville.

With regard to lakes, few infections were found in more than 100 lakes examined by one of us (L. R. R.) in south-eastern Quebec. Infected fish were found in two lakes only, *Esox niger* from Brome Lake in the Yamaska system and *Poecilichthys exilis* from Black Lake in the Becancoeur system. Both of these lakes are of the same type, being shallow, warm lakes, rich in aquatic vegetation. A lake in the Gaspe Peninsula game reserve yielded us a trout, *Salvelinus fontinalis*, and another infected trout was obtained from a private lake owned by a friend in the Laurentians, his lake being fed by a small stream with two small waterfalls on it. A casual collection of yellow perch caught by a friend in the Ouareau River near Rawdon in the Laurentians and another perch sent to us from Lake Memphremagog yielded two species of Myxosporidia. Finally, perch and Gaspe salmon (*Salmo salar*), purchased in Montreal, have provided interesting material.

As a general statement, myxosporidian infection of fresh-water fishes is most marked in the transitional zone from highland to lowland and is rare in highland waters. Slowly running and stagnant waters with an abundance of algal growth and other aquatic vegetation, and warm modified brooks running through grasslands, seem the most favourable localities for Myxosporidian infections.

The infected fish

The following fish infected with Myxosporidia have been examined:

Family Esocidae: *Esox niger*, *Esox maskinongy*.

Family Catostomidae: *Catostomus commersonii*, *Moxostoma aureolum*.

Family Cyprinidae: *Pfrille neogaeus*, *Notropis cornutus*, *N. heterolepis*, *Rhinichthys atronasus*, *Couesius plumbeus*, *Hyborhynchus notatus*.

Family Etheostomidae: *Poecilichthys exilis*.

Family Percidae: *Perca flavescens*.

Family Salmonidae: *Salmo salar*, *Salvelinus fontinalis*.

Fourteen species of infected piscine hosts have been examined, with forty-two cases of myxosporidian infections. These include twenty-five new species of Myxosporidia and several varieties, races or strains of some of them, with three already known species. Some infections of individual fish with two different genera of Myxosporidia have been observed and will be noted later. It must be stated definitely that the proportion of infected fish out of the very large numbers examined is extremely small.

Methods

When collections of fish obtained by rod and line, netting, traps or purchase were examined, any specimens that did not appear to be quite healthy were set aside and examined fresh, as soon as possible, for parasites. Especially was this the case when whitish spots or tumours were obviously present. Many such fish were examined rapidly in the field. Fresh preparations were made and examined microscopically for parasites. If such were found, and conditions

permitted, smears were made and subsequently stained. Attempts were made to induce extrusion of polar filaments, often with little success. The infected fish or appropriate portions of them were preserved, usually in formol, sometimes in 70% alcohol or in Carnoy fluid.

Smears and sections of the infected tissues were made, sections being cut at 2, 3, 4 and 6 μ thickness. The stains used were Heidenhain iron haematoxylin, long and short methods, Rosenbusch iron haematoxylin, Mallory phosphotungstic haematoxylin, Ehrlich and Delafield haematoxylin with eosin or safranin as counterstain, thionin, gentian violet and Giemsa stains. Methyl green and neutral red were very useful in examining fresh preparations. A dark-ground condenser also was of service.

All drawings were made with an Abbé-Zeiss camera lucida. For reasons of space spores have been copied with the polar capsules pointing downwards, though it is known that some authorities consider the capsular end to be anterior. All illustrations are drawn to the same scale. The dimensions of organisms given in this paper are derived from preserved material, unless otherwise stated.

THE MYXOSPORIDIA OBSERVED

The following representatives of the Myxosporidia have been found in the fresh-water fishes examined by us from Quebec waters.

Family SPHAEROSPORIDAE Davis, 1917

The Sphaerosporidae have spherical spores with two polar capsules at one end. There is no iodinophilous vacuole. The sutural line is practically straight. One species of the genus *Sphaerospora* only has been observed by us, but it has been found in two hosts, *Notropis cornutus* and *Catostomus commersonii*, from two different localities.

Family MYXIDIIDAE Thélohan, 1892

The Myxidiidae have the sutural plane of the spore either coincident with or at an acute angle to the long diameter of the spore. The spore may be fusiform or semicircular, with a polar capsule at each end. The sporoplasm may or may not contain an iodinophilous vacuole. Two of the four genera of Myxidiidae are represented in our collection, namely, *Myxidium* Bütschli, 1882 and *Zschokkella* Auerbach, 1910. In each case a new species is reported, *Myxidium percae* n.sp. from the yellow perch, *Perca flavescens* and *Zschokkella salvelini* n.sp. from the speckled trout, *Salvelinus fontinalis*.

Family MYXOSOMATIDAE Poche, 1913

The Myxosomatidae have the sutural plane of the spore as in the Myxidiidae. The spore may have two or four polar capsules and lacks an iodinophilous vacuole. The genus *Myxosoma* Thélohan, 1892 is considered by some workers to be the same as *Lentospora* Plehn, 1905, though other workers retain both

genera, the distinctions between which are difficult. The genus *Myxosoma* is used in its original connotation in this paper. Members of the genus *Myxosoma* only have been found. Several distinct species of *Myxosoma* have been found from different specimens of the same kind of host from different localities. Thus, three distinct species of *Myxosoma* have been found in *Notropis cornutus* from a brook south of Haseville, the middle branch of the Missisquoi River at Abercorn and from another site some miles below Abercorn. *Catostomus commersonii* has also yielded three species from three different localities, the Stoke River, Coaticook River and the Francoeur Brook. Two forms have been obtained from different *Pfrille neogaeus* caught in the Ulverton River.

Family Myxobolidae Thélohan, 1892

Members of the Myxobolidae resemble the Myxosomatidae, so far as bicapsular genera are concerned, except that they do not possess iodinophilous vacuoles. Also, unicapsular genera occur. Three of the four genera of Myxobolidae are represented in our collection.

Genus *Myxobolus* Bütschli, 1882. The members of this genus have the characters of the family. They are bicapsular. They have oval or ovoidal spores, without a process, and two pyriform polar capsules. Species of *Myxobolus* have been obtained from *Poecilichthys exilis*, *Esox maskinongy*, *Perca flavescens*, *Rhinichthys atronasus*, *Notropis cornutus* (three forms, from Alder Brook, Rivière des Rosières and a tributary of the Salmon River at Scotstown), *Notropis heterolepis*, *Catostomus commersonii* (two forms from the Nicolet River at Ford Village and from the Francoeur Brook), *Couesius plumbeus*, *Hyborhynchus notatus*, *Moxostoma aureolum* and *Salvelinus fontinalis*. Ten genera and eleven species of piscine hosts are thus involved.

Genus *Thelohanellus* Kudo, 1933. This genus has only one polar capsule. It was created by Kudo for *Myxobolus piriformis* Thélohan, which had a single polar capsule. The Canadian fresh-water fishes in which we have found infections are *Notropis cornutus* from two sites on the Nicolet River, Rivière des Pins, Rivière des Rosières and Alder Brook, *Pfrille neogaeus* from the Ulverton River and *Hyborhynchus notatus* from Rivière des Pins, and *Catostomus commersonii* from the Coaticook River. Local races or varieties occur, as will be shown later, but apparently only one species is involved.

Genus *Henneguya* Thélohan, 1892. Members of the genus *Henneguya* have spores with one or two appendages, sometimes termed caudal appendages or processes. Species of *Henneguya* with a single spore appendage have been observed by us from *Salvelinus fontinalis*, *Notropis cornutus* and *N. heterolepis*. It is considered that the species of *Henneguya* from *Salvelinus* and *Notropis* are probably two strains of the same species. Observations on species of *Henneguya* with forked appendages to their spores have been made on species from *Perca flavescens*, *Salmo salar* and *Esox niger*.

The greater number of Myxosporidian infections of fresh-water fishes observed by us have been infestations with a single species. However, a few

cases of cysts due to two kinds of parasite have been found. The appearance of the cysts is much alike and their nature can only be determined by microscopical examination. *Notropis cornutus*, from Alder Brook, harboured *Henneguya* and *Thelohanellus*; another from Rivière des Rosières was parasitized by *Myxobolus* and *Thelohanellus*; another from Rivière des Pins had cysts due to *Sphaerospora* and *Thelohanellus*. *Pfrille neogaeus* from the Ulverton River contained cysts of *Myxosoma* and *Thelohanellus*, and *Catostomus commersonii* from the Francoeur Brook had both *Myxosoma* and *Thelohanellus* cysts.

The species of Myxosporidia from Quebec fresh-water fishes may now be described systematically.

Family SPHAEROSPORIDAE

One species of *Sphaerospora* has been observed by us so far in Quebec fresh-water fishes.

Sphaerospora notropis n.sp.

(Pl. I, fig. 4; Pl. IV, figs. 22–43)

An interesting *Sphaerospora*, apparently new to science, has been observed in a large cyst situated below the epithelium of the roof of the mouth and protruding into the oral cavity of an adult *Notropis cornutus*, 5·8 cm. long, collected from the Rivière des Pins. This fish had a double myxosporidian infection, a large cyst due to *Thelohanellus* occurring on the left side of the dorsal fin. Subsequently, this same species of *Sphaerospora* was found in a *Catostomus commersoni*, 6·2 cm. long, collected from the Francoeur Brook, the fish having several small elongate cysts about 0·2 mm. long in its muscles.

Morphology

The youngest pansporoblasts (Pl. IV, Fig. 22) observed are uninucleate, rounded to subspherical and are 6·4–7·3 μ in diameter. The cytoplasm is homogeneous and the nucleus relatively large, with a small karyosome and a few granules of chromatin on the nuclear membrane. Multinucleate forms (Figs. 23–26) have the same type of nuclei. Tetranucleate organisms (Fig. 23) sometimes have large granules of extra nuclear chromatin.

The pansporoblasts may produce one or generally two sporoblasts. Such is shown in Fig. 24, where two groups of seven nuclei are present, and cytoplasmic segregation around the groups has begun. Later stages showing the formation of polar capsules and differentiation of nuclei have been observed (Figs. 25–29), the sporoplasmic nuclei being larger than either the capsulogenous or parietal nuclei, and possessing distinct karyosomes.

The spores (Figs. 30–43) show some variation in appearance but many of them are almost spherical. Others are oval and all stages of transition between the two outlines and shapes have been observed. The sporocyst or valves are delicate and the spores are rather easily deformed by mutual pressure or by manipulation. The spores are 9–11·4 μ long and 9–9·5 μ broad. Many are subspherical and about 9·5–10 μ in diameter. None shows any trace of an

iodinophilous vacuole. The valves are smooth and homogeneous in appearance. The suture is straight or slightly curved (Fig. 42), never sinuous as in *Sinuolinea* Davis, and the two valves are approximately the same size. The parietal or valvular nuclei are small rounded bodies, usually two in number (Figs. 33, 34, 37), but one larger oval one may be present (Fig. 31).

The polar capsules are pyriform, with fairly broad ends (Fig. 42). They vary in size, the range being 2·7–5·5 μ long and 1·8–3·6 μ broad. They are about half the length or rather more than half the length of the spore in the majority of cases. The capsulogenous nuclei are small rounded bodies (Fig. 34) or compact small masses (Figs. 36, 38, 40). The polar filaments are fine and form a series of folds within the polar capsules (Figs. 32, 37, 38, 40). Fully discharged filaments have not been observed, but partly discharged ones (Fig. 43) from spores showing some signs of collapse, due to their discharge, have measured up to 45 μ.

The sporoplasmic nuclei are clear distinct karyosomatic bodies, some showing a few chromatin granules on the nuclear membrane, others being without them. They may lie transversely parallel to one another (Figs. 33, 36, 37) or almost tandem (Fig. 35). The sporoplasm forms a compact mass and has no iodinophilous vacuole.

Systematic position

The myxosporidian under discussion has no iodinophilous vacuole in its spores and the spores are approximately spherical in most cases. This would place the organism in the genus *Sphaerospora*, though some of the more oval spores resemble *Myxosoma*. On the whole, the characters are such as to place it in the genus *Sphaerospora*. With regard to the species, no *Sphaerospora* has hitherto been recorded from either *Notropis cornutus* or *Catostomus commersonii* as far as can be ascertained from the literature at our disposal. Thélohan (1895), when defining the genus *Sphaerospora*, noted that they could be considered as Leptotheca of which the spores had become spherical by curving of the bivalvular axis. *Sphaerospora divergens*, then described by him, had spores not quite circular, some being 12 by 10 μ, that is, larger than those of the Canadian species. *S. rostrata* and *S. divergens* are species with striated spores, also *S. polymorpha* Davis and *S. angulata* Fugita. *S. carassii* Kudo, 1920, from *Carassius carassius* in Japan, has smooth spores, 8–13 μ in diameter, polar capsules 4–5 μ by 2·5–3·5 μ, and it has a coarse polar filament of few coils, judging from Kudo's illustrations. Thélohan (1895) has described *Sphaerospora elegans* from the kidney tubules and ovarian connective tissue of the sticklebacks, *Gasterosteus aculeatus* and *G. pungitius*, and in this form the sutural ridge projects to form a sort of spine. The spores of *Sphaerospora elegans* were about 10 μ in diameter on the average. Schuurmans-Stekhoven has also described *Sphaerospora gasterostei* for a small *Sphaerospora* with spores 5·3–8·2 μ long and 5·6–8·5 μ broad. Fantham (1930) described *S. subelegans* from the stockfish *Merluccius capensis* in South Africa. This has simple, thin-walled

subspherical spores, 9–13·6 μ in diameter, the sutural diameter being slightly the smaller. Léger (1930) has described *Sphaerospora pernicialis* causing epidemics among young tench in France. The spores of this species are 8–8·75 μ in diameter, a few being only 7 μ, while the polar capsules are 2·5–3 μ long. The polar filaments have four spiral turns. It is clear that the species of *Sphaerospora* from *Notropis cornutus* and *Catostomus commersonii* in Canada does not conform exactly in dimensions or appearance with any of the species discussed, which appear to be its nearest allies. Perhaps its nearest affinity is with *Sphaerospora subelegans*, which occurs in South African marine fish. However, as its dimensions differ and the host-parasite relation and geographical distribution also may be of significance, it seems best to consider it a new species and for purposes of reference it is named *S. notropis* n.sp., with characters as herein set forth.

Family MYXIDIIDAE

One species of the genus *Myxidium* and one of the genus *Zschokkella* have been found by us in our collection of Canadian fishes.

Myxidium percae n.sp.

(Pl. II, figs. 1–10)

An interesting *Myxidium* has been observed from a yellow perch, *Perca flavescens*, taken from the Ouareau River near Rawdon, Quebec. A small, conical cyst, 1–1·5 mm. in diameter, was present beneath the skin at the angle of the right pectoral fin. A very small quantity of milky fluid exuded from the cyst on pressure. When examined microscopically, a few spores and trophozoites of a *Myxidium*, together with pus cells and much broken-down tissue, were detected. This was the only fish out of fifteen collected at the same time that harboured the parasite. About 200 yellow perch have been examined since then from several sources, but this is the only case of infection, and the degree of infection was slight.

Morphology

It is regretted that large trophic forms of the parasite were not present in this specimen.

Young pansporoblasts with a single nucleus were not abundant. Some binucleate forms were present. The parasite appears to be disporous. Pansporoblasts showing segregation and differentiation of nuclei (Figs. 1, 2) may attain 21 μ in diameter. The nuclei of the developing spores show differentiation, the future sporoplasmic nuclei being larger than the others, the parietal or valvular nuclei smaller and more elongate and the capsulogenous nuclei smaller and round.

The spores (Figs. 3–10) are elongate and curved, somewhat resembling an integration sign. They are 14·5–20·9 μ long and 2·3–6 μ broad, the maximum length being unusual. Most of the spores did not exceed 4·5–5 μ in breadth.

The sutural line and ridge are curved (Fig. 8), following the contour of the spore. The surface of the valves has about five longitudinal striae (Figs. 5–9).

The polar capsules are situated one at each end of the spore; they are elongate pyriform in shape (Figs. 2–9). They are 5–7·3 μ long and 1·8–3·2 μ broad. In some spores the polar capsules are of slightly different sizes (Figs. 7, 9). The capsulogenous nuclei are rounded (Figs. 2, 3) and, with age, they shrink into small compact chromatoid masses (Fig. 5). The valvular nuclei, when discernible (Fig. 4), are rather elongate-oval structures.

The sporoplasm is granular and homogeneous. The sporoplasmic nuclei are two in number and are rounded karyosomatic bodies (Figs. 3, 4). Sometimes they are parallel, across the short diameter of the spore (Figs. 2, 3, 4, 7), occasionally they are arranged one behind the other (Fig. 6), while they may be at different levels from each other (Fig. 8).

Some free amoebulae have been observed (Fig. 11). They are small organisms, convex above, concave below, with hints of pseudopodia. Those measured were about 4–4·5 μ in diameter.

Systematic position

The present record of *Myxidium* in *Perca flavescens* appears to be the first notification of infestation of Canadian yellow perch by a myxosporidian parasite. Kudo (1934) has reported that his examinations of 103 *Perca flavescens* were negative for Myxosporidia. We have not been able to trace any reference to the occurrence of *Myxidium* in European perch, *Perca fluviatilis*. Also, the present seems to be the first record of the subcutaneous infection of a fresh-water fish with *Myxidium* from the North American Continent, though Jameson (1931) has found *M. oviforme* in the gall bladder of a rainbow trout, *Salmo irideus*, in California. The spore of *Myxidium oviforme* is quite different from that of the perch parasite. With regard to other possible affinities, Ishii (1915) has described *M. anguillae* from the subcutaneous tissue of *Anguilla japonica* in Japan,[1] but this is not the same as the *Myxidium* of the yellow perch, the spores of *M. anguillae* being 9·1 μ long and 2·8 μ broad, which is considerably smaller than those of the *Myxidium* of the yellow perch, while the spore structure is different in the two cases. While the length of the spore of the perch *Myxidium* is much the same as that of *M. bergense* Auerbach 1910, from various marine fishes, the breadth of the spore is considerably less and the range of lengths of the polar capsules is greater. *M. bergense* has been recorded in Canada from the gall bladders of the haddock (*Melanogrammus aeglefinis*) by Mavor (1916) and by Ellis (1930) from the haddock and the hake (*Urophycis tenuis*), both marine fishes, and all caught at St Andrews, New Brunswick, Canada. The proportions of the lengths of the polar capsules to those of the spores is different in *Myxidium bergense* and the *Myxidium* of the yellow perch. In 1919 Johnston & Bancroft described *M. therapon* from *Therapon carbo* and *T. hillii* in the Brisbane River, Australia. The spores are lenticular, 9–10 μ

[1] We gratefully thank Dr Ijima for translations of the Japanese texts.

long by 4 μ wide, and the polar capsules are 2–3 μ by 1·2 μ. It certainly is different from the present Canadian form. The spores of the *Myxidium* of the yellow perch approximate in size and morphology with those described but not named specifically by Fantham (1919*a*, *b*) from the bile of the South African marine fishes, *Clinus taurus*, *Dentex argyrozona*, *Cantharus blochii* and *Clinus cottoides*. The very different situation of the parasite of the yellow perch and its absence from the gall bladder show great physiological dissimilarity between the two organisms. The spores are very different from those of *Myxidium pagelli* Fantham 1930 and *M. parvoviforme* Fantham 1930, also from South African marine fishes and occurring in the bile. Schuurmans-Stekhoven (1920) has described *M. rhomboideum* from *Gasterosteus pungitius* and *G. aculeatus*, but the Canadian form cannot be this species, of which the spores are only 7·7 μ long.

From the foregoing considerations, the *Myxidium* from *Perca flavescens* is considered to be a new species, distinguished from other species of *Myxidium* by its morphology, its site of occurrence and its host. It is designated *M. percae* n.sp., with characteristics as herein set forth.

Zschokkella salvelini n.sp.

(Pl. II, figs. 11–19)

An apparently new species of *Zschokkella* has been observed, the host being a speckled trout, *Salvelinus fontinalis*, caught in a small private lake near Lantier, Quebec. The viscera were examined for animal parasites. During the course of the examination, a minute cyst attached to the posterior end of the kidney was found. On rupturing the cyst, a myxosporidian was found, but the host had already reacted against the parasite, for the cyst was partly calcified. Examinations of the urinary bladder, gall bladder, peritoneum, gut and other internal organs were negative.

Morphology

Owing to the onset of calcification and paucity of material, only a few stages of the parasite have been observed.

Binucleate pansporoblasts (Fig. 12) are more or less subspherical, and are up to 9·5 μ in diameter. The cytoplasm is finely granular. The two rounded karyosomatic nuclei show small granules of chromatin on the nuclear membranes.

The sporoblasts (Figs. 13, 14) are relatively large and those seen were monosporous. They were 17·3–18·2 μ long and up to 13·6 μ deep or broad. The nuclei show morphological differentiation, large nuclei with karyosomes and beaded nuclear membranes being the sporoplasmic nuclei, elongate-oval nuclei being valvular or parietal and smaller rounded ones the capsulogenous nuclei. The polar capsules, when differentiating, appear as refractile rounded areas in life.

The spores (Figs. 15–19) are somewhat helmet-like, one margin being but very slightly curved and the other markedly curved. The valvular margins project at the polar capsules. Seen at right angles to the front view, along the sutural line, they are somewhat ellipsoidal (Fig. 18). The spores are 10·9–14·5 μ broad and 19·1–21 μ from tip to tip of the polar capsules. The suture is sinuous (Fig. 18).

The polar capsules appear more or less spherical (Figs. 15, 19), if their short ducts be disregarded, but are pyriform if the ducts are included. Sometimes the ducts are bent at an angle to the body of the spore (Figs. 17, 18). Measured with the ducts, the polar capsules are 7·3–9·5 μ long and 5–6·4 μ broad. The polar filaments are folded in many fine figure-of-eight coils within the polar capsules (Figs. 17, 18). Partly extruded filaments measured have been up to 35 μ in length; one such partly extruded filament is shown in Fig. 19. Fully extruded filaments have not been observed.

The sporoplasmic nuclei (Figs. 15, 17–19) are large, with distinct karyosomes and well-marked chromatin granules on the nuclear membranes. In a young spore the capsulogenous nuclei are small rounded distinct bodies, which gradually decrease in size and persist as small compact chromatin bodies (Figs. 17–19). The valvular or parietal nuclei (Fig. 15) are more or less elongate-oval as in the sporoblasts, but disappear with age.

Systematic position

The speckled trout, *Salvelinus fontinalis*, is recorded for the first time as a host for a species of *Zschokkella*. The genus *Zschokkella* was instituted by Auerbach in 1910, *Z. hildae* being his type species. This was obtained from the urinary bladders of various marine fish, chiefly Gadidae. *Z. hildae* is larger than the Canadian species and has many small differences in morphology, particularly in respect to its polar capsules. Klokacewa (1914) described *Z. nova* from the gall bladder of *Carassius*, but its spores are much smaller than those of the parasite of the speckled trout. Davis (1917) has described *Zschokkella globulosa* from the urinary bladder of *Spheroides maculatus*, the spores of this species being 17 by 7 μ. They are thus much smaller than those of the parasite under discussion, as well as showing morphological differences. *Zschokkella acheilognathi* Kudo, 1916 (summarized by Kudo, 1920, p. 123), from the gall bladder of *Acheilognathus lanceolum* in Japan, has smaller spores and differs considerably in appearance from the form in the speckled trout. Nemeczek (1922) has described *Zschokkella rovignensis* from species of *Scorpaena* obtained at Rovigno, Italy. This has much larger spores, with different proportions from those of the trout parasite. An interesting cytological point is that four chromosomes have been found as a constant feature in all stages of *Zschokkella rovignensis*. We regret that our material was too limited for extended cytological investigations. The nearest affinity of the *Zschokkella* from *Salvelinus fontinalis* appears to be *Zschokkella hildae* Auerbach, but it differs as already indicated.

It cannot be assimilated with any other species as shown in the foregoing. It is therefore considered to be a new species and is named *Z. salvelini* n.sp., with characters as herein described.

Family MYXOSOMATIDAE Poche, 1913 emend. Kudo

Eight species of the genus *Myxosoma* have been found by us in fresh-water fishes in Quebec Province.

Myxosoma notropis n.sp.

(Pl. I, fig. 3; Pl. II, figs. 20–36)

An adult red-fin shiner, *Notropis cornutus*, 6·8 cm. long, infected with a species of *Myxosoma*, was found in a collection made from the first brook south of Haseville in the Yamaska watershed. This fish contained a large cyst that filled and distended the anterior part of the abdomen and forced the gut ventrally and laterally. The liver had also been invaded and its structure and identity had become almost obliterated by the parasite, which had created the condition of hepatic tumour (Pl. I, fig. 3).

Morphology

The morphology of *M. notropis* n.sp. is as follows:

The amoebulae (Figs. 21, 22) are binucleate and vary somewhat in shape. Those measured were 6–7·5 μ by 7·5–9·3 μ. Ectoplasmic lobose pseudopodia are present. The endoplasm is granular and homogeneous.

Uninucleate pansporoblasts are small, more or less rounded bodies, from about 4 μ in diameter. Binucleate forms are rounded or elongate (Fig. 23) and vary from about 5–8·6 μ. Well-developed multinucleate forms are considerably larger. A young multinucleate form is shown in Fig. 24. Ths nuclei are rather large and karyosomatic. Extranuclear chromatin may be present. Other multinucleate forms are shown in section in Fig. 20.

The sporoblasts are rounded to somewhat irregular in shape (Figs. 25–27). They are disporous. Young sporoblasts show up to seven nuclei which are already differentiated (Fig. 25), small rounded nuclei being sporoplasmic, valvular or parietal nuclei being more elongate and those of the polar capsules smaller than the others. Beginnings of polar capsules may also be discerned (Fig. 26). In an older form polar capsules are more developed and segregation into two spores can be seen (Fig. 27).

The spores (Figs. 28–36) are oval in outline and ovoid in build, the end with the polar capsules, termed the anterior end by some, being narrower than the opposite pole. They are 13·3–16·6 μ long and 6·4–11 μ broad. The sporocyst is fairly thick. The sutural ridge is somewhat thin and slightly curved (Fig. 20). The valvular nuclei in the younger spores are relatively large, elongate-oval bodies. One (Fig. 28) or two (Figs. 31, 32, 36) have been seen, two being the typical number. In one case three valvular nuclei were present (Fig. 29).

Differential degeneration may occur, causing the presence of one nucleus. In older spores, as usual, the valvular nuclei gradually become smaller and compact (Fig. 28) and gradually disappear.

The polar capsules are elongate-pyriform, with short ducts. They may be equal (Figs. 29, 30, 31, 36) or subequal (Figs. 28, 33). They are 4–6·4 μ long and 1·8–3·2 μ broad. The capsulogenous nuclei are rounded bodies (Fig. 31) but gradually become smaller and more compact (Figs. 29–32) and in some spores disappear. The polar capsules in some cases show fine coiled or looped polar filaments (Figs. 33–35). Extruded polar filaments have not been seen.

The sporoplasm is finely granular and may form a compact mass (Figs. 28, 29, 35), or its edges may be prolonged outwards in a radiating manner (Figs. 30, 33, 34), suggesting fine pseudopodia. The sporoplasmic nuclei are distinct and karyosomatic. They may be near together, parallel to the short axis of the spore (Fig. 35), but more often are arranged tandem (Fig. 28) or obliquely tandem (Figs. 31, 32, 36).

Systematic position

As *Notropis cornutus* is stated to be widely distributed on the North American Continent, it was considered likely that this *Myxosoma* had already been described. Search of the literature shows that such is not the case. As far as we can ascertain, Gurley (1893, 1894) described no such form from *Notropis cornutus*. Kudo (1934) has given an account of *Myxosoma robustum* from *Notropis cornutus* from Illinois, U.S.A., but *Myxosoma robustum* shows considerable differences from the present Canadian specimen, both in structure and range of dimensions, the Canadian species having the greater range, particularly as regards breadth. The spore of *M. robustum* has thickenings or striae on its sutural edge and these have never been seen in the Canadian form.

Though careful comparison has been made with species of *Myxosoma* from other hosts, there is no species with which the *Myxosoma* from *Notropis cornutus* here described can be assimilated. It is, therefore, considered to be a new species and is designated *Myxosoma notropis* n.sp., with characters as herein given.

Myxosoma commersonii n.sp.

(Pl. III, figs. 1–7)

A very small cyst in the skin of the dorsal surface of the body of a *Catostomus commersonii* caught in the Stoke River contained an interesting *Myxosoma*, pansporoblasts, sporoblasts and a few spores being observed.

Morphology

The youngest pansporoblasts observed were already multinucleate (Figs. 1, 2), the nuclei showing some differentiation in size and shape. They had well-marked nuclear membranes. Chromatin was deposited as fairly heavy granular masses on the nuclear membranes. Some nuclei showed mitoses in progress.

Stages in the differentiation of sporoblasts are shown in Figs. 3–5. Usually the pansporoblast forms two spores in two sporoblasts. The amount of chromatin at this time increases. Each sporoblast produces one spore. The differentiation of the two sporoblasts may not synchronize, and sometimes polar capsules of one spore are present (Figs. 3, 5) before there is any trace of those of the second spore.

Young spores (Fig. 6) have finely granular, homogeneous cytoplasm. Their sporoplasmic nuclei stain well and often show four chromatin thickenings on their nuclear membranes. Orientation of the organelles within the young spore is sometimes irregular.

The mature spores (Fig. 7) are oval bodies with moderately thick sporocysts. The valves are smooth and there are neither folds nor thickenings. The sutural ridge is thin, curved and uniform. The sutural line is indistinct. In the young spore the valvular nuclei are large oval to lenticular bodies (Fig. 6), but they disappear with age. The spores vary considerably in size, being 9·5–16·5 μ long and 7–11·4 μ broad.

The polar capsules are elongate-pyriform bodies, up to 7·7 μ long and 3·2 μ broad. They are almost or quite half the length of the spore. The capsulogenous nuclei are small and compact. Fine polar filaments are present; they have closely wound coils (Fig. 7). Extruded polar filaments have not been observed.

The sporoplasm forms a rather compact mass. The sporoplasmic nuclei stain well, showing four thickenings of chromatin on their nuclear membranes, and have small, sometimes excentric, karyosomes.

Systematic position

Gurley (1894) has described a myxosporidian from beneath the skin of *Erimyzon sucetta oblongus* (= *Catostomus tuberculatus* of other authorities) from North Carolina and the Fox River, Mississippi. He named the parasite *Myxobolus oblongus*. It would now be placed in the genus *Myxosoma*. The organism that we have described is not *Myxobolus oblongus*, since it differs in having a very different range of dimensions of spores, which also have not the characteristic "spatular, approaching roundish oblong" shape of *M. oblongus*. Kudo (1926) has described *Myxosoma catostomi* from *Catostomus commersonii*, but the species we have observed is not *Myxosoma catostomi*, from which it differs in having larger polar capsules, finer, more closely coiled polar filaments and in not having triangular thickenings on the sutural ridge such as characterize *M. catostomi*. Comparison with other *Myxosoma* from *Catostomus commersonii* described later in this paper show constant differences, and the organism does not agree with species of *Myxosoma* from piscine hosts in Europe. While deploring the multiplication of new species it seems inevitable, if only for purposes of reference. We therefore designate this organism *M. commersonii* n.sp., with characters as herein set forth.

Myxosoma orbitalis n.sp.
(Pl. I, fig. 5; Pl. III, figs. 8–22)

Among a number of *Notropis cornutus* collected from the middle branch of the Missisquoi River below Abercorn was one with three cysts, situated deep in the orbit, extending down over the cheek, bulging outwards and upwards and forcing the eye out latero-dorsally, carrying the suborbital ring with it (Pl. I, fig. 5). Smears and sections of the cysts showed that the tumours were due to the same species of *Myxosoma*.

Morphology

The general impression gained on examination of the *Myxosoma* is that of a rather delicate species with relatively large spores. The cyst was fairly stout, with a firm capsule of fibrous tissue on the outside.

Uninucleate pansporoblasts (Figs. 8, 10) are oval to somewhat wedge-shaped bodies, with finely granular homogeneous cytoplasm. The nuclei are prominent, with karyosomes and occasionally chromatin granules on the somewhat delicate nuclear membranes. The uninucleate pansporoblasts were 3·6–9·5 μ by 2·2–6·8 μ. Binucleate forms (Fig. 9) showed much the same structure and were up to 11 μ in diameter. Tetranucleate and multinucleate pansporoblasts were fairly numerous in the preparations. They vary from rounded to irregular in contour, some of the larger ones being 25 μ in diameter. Various stages of division of the nuclei have been seen (Fig. 11). Large pansporoblasts (Fig. 12) may contain several sporoblasts in various stages of differentiation at the same time. When sporoblasts are well formed they may separate from the pansporoblast and become free, or they may form two spores while within the mother cell. A sporoblast with one sporoplasmic nucleus as yet undivided but having more chromatin than the other nuclei is shown in Fig. 13. Cytoplasmic segregation around this nucleus is also beginning. In old sporoblasts the constituents of two spores can be seen (Fig. 14). Often the sporoplasm around the sporoplasmic nuclei forms a distinct mass, and the two polar capsules of each spore can be seen. The ducts of the polar capsules sometimes can be better demonstrated in these immature developing spores than in those in which the valves are well formed.

The spores (Figs. 15–22) are oval to slightly ovoid bodies, being 13·3–17·5 μ long and 8–12 μ broad. The spores are delicate in appearance, despite their size. The valves are transparent and without markings or thickenings. Occasionally oval valvular or parietal nuclei are seen, sometimes one large one (Figs. 19, 20) or one or two small ones (Figs. 18, 21) being present. In many younger spores one large valvular nucleus only was observed and, as usual, they disappear in older spores.

The polar capsules are pyriform bodies, 4·1–6·4 μ long and 1·8–3 μ broad. They usually stain densely (Figs. 15–19). In some spores a somewhat loosely coiled polar filament can be seen (Figs. 20, 21). The capsulogenous nuclei

observed (Figs. 15–19) have usually been small compact masses of chromatin, often situated near or forming a cap to the rounded end of the polar capsule. Fully extruded polar filaments have not been seen, but partly extruded ones (Fig. 22) may reach 43 μ in length.

The sporoplasm is clear, very finely granular and homogeneous. It usually forms a compact well-defined mass around the sporoplasmic nuclei. Small individual masses of sporoplasm may be present as triangular masses extending beyond the capsulogenous nuclei (Figs. 15, 16). The sporoplasmic nuclei vary in size in different spores. Usually they are of medium size (Figs. 15–19), karyosomatic and have well-marked nuclear membranes with small deposits or thickenings of chromatin. In a few spores larger and less well-defined sporoplasmic nuclei were present (Fig. 20).

Systematic position

The present investigation has resulted in the discovery of three species of *Myxosoma* as tissue invading parasites of *Notropis cornutus* from various localities and each appears to be distinct. Gurley (1893) combined the genera *Sphaerospora* and *Myxosoma* under the name *Sphaerospora* and considered *Sphaerospora* to be a subgenus of *Chloromyxum*. He did not record any *Sphaerospora* from *Notropis cornutus*, nor has examination of his numerous illustrations revealed any form like the *Myxosoma* here described. Thélohan (1895) described two organisms as *Myxosoma*, *M. dujardini*, which occurred on the gills of *Scardinius erythrophthalmus* and *Leuciscus rutilis*, and *Myxosoma ambiguum*, found in the urinary bladder of *Lophius piscatorius*. These parasites of marine fishes are quite distinct from the *Myxosoma* of *Notropis cornutus*. Davis (1917) found no *Myxosoma* in the various fishes he examined from the Beaufort region of North Carolina. Kudo (1920) lists no Myxosporidia from *Notropis cornutus*, nor did he find *Myxosoma* in other species of *Notropis*, though he records in 1934 the occurrence of *Thelohanellus notatus* in *Notropis cornutus* in Illinois. Plehn (1924) lists no *Myxosoma* in her book on fish diseases. The possibility of *Myxobolus oblongus* being *Myxosoma catostomi* has already been discussed in connexion with *M. commersonii*, and the same considerations apply here. It becomes necessary to create a new species for this *Myxosoma* from *Notropis cornutus* and the name *Myxosoma orbitalis* n.sp. is given to it, the species name being with reference to its occurrence in the orbit of the host. Its characteristics are as here set forth.

Myxosoma pfrille n.sp.
(Pl. III, figs. 23–37)

A specimen of *Pfrille neogaeus* from the Ulverton River, St Francis watershed, had a large abdominal tumour or cyst occupying the dorsal half of the cavity posteriorly and taking up much of the space normally filled by the air bladder. The cyst projected anteriorly on the right side as a sort of wing lateral to the lobe of the liver and also had a solid broad portion between the

liver and the stomach. On examination the tumour was found to be due to a myxosporidian of the genus *Myxosoma* and to be a hitherto unrecorded form, as far as we could ascertain from the literature on the subject. It is, therefore, designated *M. pfrille* n.sp., its systematic position being discussed later.

Morphology

M. pfrille was studied in sections from each part of the tumour and in wet preparations. The cyst was bounded by a tough wall of connective tissue, in which muscle fibres and their nuclei were also present. Among the fibres very young pansporoblasts were scattered in small numbers, and close to the innermost fibres rounded uninucleate pansporoblasts were present, often in only one layer but sometimes several layers deep. Vacuolated alveolar cytoplasm was present between the young parasites (Fig. 23).

Small binucleate amoebulae are 4–8 μ long and 2·7–5·5 μ broad. Their cytoplasm is homogeneous and their nuclei karyosomatic (Fig. 26).

Pansporoblasts (Figs. 23, 24), when uninucleate, are more or less rounded, with homogeneous cytoplasm and nuclear membranes with little chromatin and small but distinct karyosomes. The nuclei of multinucleate pansporoblasts appear to have more chromatin deposited on their nuclear membranes (Figs. 30, 31). Multinucleate pansporoblasts at first are rounded, five to seven nuclei being at first produced by division. In some rather older specimens early segregation within the pansporoblast of two sporoblasts can be observed (Fig. 27), and the cytoplasm of the pansporoblast may be distinctly alveolar. In other cases the cytoplasm is practically homogeneous (Fig. 28) with a tendency to segregate around two pairs of nuclei which are those of the two potential sporoplasmata. Such forms may be 20 μ long and 13·2 μ broad. In later stages polar capsules of spores can be seen (Figs. 28, 29), sometimes showing as oval cells with striae representing the differentiating polar filaments, and sometimes staining uniformly without indication of the structure of the polar filaments. Sporoplasmic nuclei can be distinguished early, as they are karyosomatic and have chromatin deposited on their nuclear membranes, sometimes with strands connecting such chromatin to the karyosomes. The future capsulogenous nuclei are small and karyosomatic. Usually two spores develop at a time.

The spores are ovoid bodies with thick sporocysts and folds or thickenings at the broader end of the spore (Figs. 32–35), and are 12·7–19·1 μ long and 7·7–11·4 μ broad. The valves are smooth and the suture is very slightly curved (Fig. 37). The valvular or parietal nuclei are usually two in number and are oval compact structures.

The polar capsules are pyriform and are 4·5–6·4 μ long and 1·8–3·2 μ broad. They have short ducts (Figs. 32, 33, 36) and a somewhat squat build (Figs. 32, 33). The capsulogenous nuclei (Figs. 34, 35) may be karyosomatic or composed of compact chromatin. One capsulogenous nucleus of each type is shown in Figs. 34. Fully extruded polar filaments have not been observed, but spores

with partly extruded polar filaments (Figs. 36, 37) have been seen, such extruded portions being up to 45 μ in length.

The sporoplasm is homogeneous and almost fills the spore. The two sporoplasmic nuclei are karyosomatic with well-marked nuclear membranes, some chromatin being deposited in the form of granules on the membranes.

Systematic position

Search of the literature has shown no reference to the occurrence of *Myxosoma* in *Pfrille neogaeus*, though Plehn (1924, p. 435) mentions that *Myxobolus mulleri* is not very frequent in the ovarium of a *Pfrille* (species not stated). The structure of the multiplicative stages and the thickenings of the spore wall differentiate the *Myxosoma* of *Pfrille neogaeus* from *Myxosoma notropis*, *M. commersonii* and *M. orbitalis* herein described. The range of dimensions falls within those of *M. grandis* Kudo, 1934 from the silver-mouthed minnow, *Erecymba buccata*, but the parasite differs in having ovoid spores with heavy thickenings and in having smaller polar capsules, those of *Myxosoma grandis* being 6–7 μ by 2·5–3 μ, while those of the *Myxosoma* of *Pfrille neogaeus* are 4·5–6·4 μ by 1·8–3·2 μ, the majority being about 5·5 μ in length. No European *Myxosoma* with which we are acquainted conforms to the description of this *Myxosoma* from *Pfrille neogaeus*, and for the foregoing reasons it is considered to be a new species and is named *Myxosoma pfrille* n.sp., with characters as set forth in the preceding.

Myxosoma media n.sp.

(Pl. I, fig. 1; Pl. III, figs. 38–51)

Among the *Notropis cornutus* taken from the middle branch of the Missisquoi River at Abercorn village, one was found with a cyst filling the dorsal portion of the abdomen and extending laterally on one or both sides of the gut (Pl. I, fig. 1). The cyst was found to be myxosporidian in character, a species of *Myxosoma* with medium-sized spores and relatively long polar capsules being present.

Morphology

The young pansporoblasts (Figs. 38, 39) are rounded uninucleate organisms, each with a relatively large nucleus containing a small but distinct karyosome. Chromatin thickenings may or may not occur on the nuclear membranes. Such uninucleate forms are usually 4·5–6·8 μ by 4·5–5·5 μ; occasionally somewhat larger or somewhat smaller uninucleate forms have been observed but they are uncommon. Binucleate pansporoblasts (Fig. 40) show an increase in the amount of chromatin in the nuclei, and in young multinucleate forms (Fig. 41) chromatin granules, which appear to be the developing karyosomes of nuclei, may be present. Some multinucleate pansporoblasts are very delicate in appearance (Fig. 42). Apparently the pansporoblasts produce two sporoblasts (Fig. 43) in which the orientation of the polar capsules and nuclei at first may not be quite regular. Each sporoblast produces one spore.

The spores are usually ovoid (Figs. 44–48) but occasionally a more angular spore (Fig. 49) may be found, this usually occurring where a number of spores are crowded together, its shape being ascribed to pressure effects. They are 11–16·8 μ long and 7·7–10·4 μ broad. The valves are smooth and without thickenings. One or more oval parietal nuclei may be present (Fig. 50) or they may be reduced to rod-like masses (Figs. 45, 46) or may not be discernible (Figs. 47, 48), having disappeared when their functioning was ended.

The polar capsules are elongate pyriform bodies, being 5–8·2 μ long and 1·8–3·2 μ broad. The polar capsules in unstained spores appear to occupy about half the length of the spore, and in stained smears the same proportion is noted (Figs. 47, 48, 51). The capsulogenous nuclei are at first small, rounded and karyosomatic (Fig. 45) but become small compact chromatin masses (Figs. 46, 47, 51). The polar filaments, as seen within the capsules, form fine, close loops. Extruded polar filaments have not been found.

The sporoplasm is homogeneous and usually forms a compact mass (Figs. 46–50). Rarely, a form showing sporoplasm with pseudopodia-like processes has been observed (Fig. 51). The sporoplasmic nuclei are usually two in number and are of medium size. They are karyosomatic, with slight thickenings on the nuclear membranes. Very occasionally a spore with but one large sporoplasmic nucleus has been found (Fig. 48). The sporoplasmic nuclei may be arranged transversely across the spore (Figs. 46, 47, 50) or may be tandem or slightly obliquely tandem in position (Figs. 44, 45, 49).

Systematic position

This *Myxosoma* from *Notropis cornutus* from the Missisquoi River at Abercorn differs from those observed in other Canadian fishes in its dimensions and in having relatively long polar capsules. Apparently it has not been reported before on the American Continent. It differs from *Myxosoma catostomi* Kudo in having a different range of dimensions of the spores, which have no thickenings on the spore wall and in having finer polar filaments with more coils. There are also many differences in the multiplicative stages of the two organisms. We cannot establish its identity with European forms of *Myxosoma*. For the present it is considered to be a new species and is designated *M. media* n.sp., with characters as herein set forth.

Myxosoma ellipticoides n.sp.
(Pl. III, figs. 52–60)

Among a collection of *Catostomus commersonii* from the Coaticook River (St Francis watershed), one fish, 9 cm. long, had five myxosporidian cysts, 5–8 mm. in diameter, on each side. On the left side five larger cysts were present on the anterior face of the cleithrum, projecting forwards and outwards. No obvious invasions of tissue behind the cysts had occurred. On the right side there were five smaller but similar cysts. On both sides the largest cysts were

in the middle and the operculum was forced out of its normal position by them. Most of the cysts were found to contain spores of a *Myxosoma*; the other cysts contained *Thelohanellus*.

Morphology

The cysts proved to be in a late stage of development. A few young uninucleate pansporoblasts only have been detected. These are about 2·7–3·6 μ in diameter, have homogeneous cytoplasm and small karyosomatic nuclei with well-marked uniform nuclear membranes. Binucleate pansporoblasts (Fig. 52) are somewhat larger and are more or less oval. One sporoblast appears to be formed at a time, but examination of younger material is necessary before definite statements can be made on this point. Pansporoblasts with seven nuclei (Fig. 53) have been found, being 7·3–11·4 by 5·5–10·9 μ. Their cytoplasm is finely granular and their small nuclei have karyosomes.

The spores are ovoid or ellipsoidal in outline, of medium size, and 11·4–14·1 μ long and 6·8–8·2 μ broad. The valves are smooth, without thickenings or folds. Valvular nuclei are oval, are of various sizes and are conspicuous (Figs. 55, 56, 59). Two usually are present.

The polar capsules are less than half the spore in length, are rather flask-like and have relatively long ducts (Figs. 57, 58), being 4·5–5·9 μ long and 1·8–3·2 μ broad. The capsulogenous nuclei are at first round and karyosomatic, when they are almost as large as the sporoplasmic nuclei (Fig. 57), but become small and compact (Figs. 54, 55). Fine polar filaments are sometimes demonstrable coiled within the capsules (Fig. 60).

Systematic position

With regard to the systematic position of this *Myxosoma*, the general morphology excludes it from being *M. catostomi* Kudo. At first it was thought that perhaps this was a small strain of *M. media* from *Notropis cornutus*, but there are morphological differences, as well as differences in dimensions. The spores of *Myxosoma media* are ovoidal, those of the present form are ellipsoidal, and most of them are almost bilaterally symmetrical. Physiological adaptation to a new host could hardly explain such differences and it is considered advisable to give the *Myxosoma* from *Catostomus commersonii* from the Coaticook River specific status, if only for purposes of reference. It is, therefore, designated *Myxosoma ellipticoides* n.sp., with characters as herein stated.

Myxosoma parellipticoides n.sp.

(Pl. IV, figs. 1–6)

Some specimens of *Pfrille neogaeus* were collected from a weed-choked slow-running brook, with very little flow, that discharged into the Ulverton River, forming part of the St Francis watershed. One of these *Pfrille neogaeus*, a gravid female 6·5 cm. long, had a massive cyst, about 10 mm. long, in the posterior half of the abdomen, that extended between the ovary and the small

intestine and forced the gut down ventrally. Apart from a very slight swelling on the right side, the presence of the cyst was not obvious externally. The cyst was soft and its contents almost milky in consistency. On microscopical examination it was found that the apparently large single tumour was really a compacted aggregate of several smaller ones, that had fused to form a composite mass. One of these smaller tumours was caused by a species of *Myxosoma*, the remainder by a species of *Thelohanellus*. In the case of the part of the compound cyst due to *Myxosoma*, a considerable amount of calcification had occurred, and the spores, normal or calcified, were lying in a fluid matrix. From the developmental phase of the parasite and the degree of degeneration of the cyst contents, it is inferred that the infection was of long standing and was nearing its end. Also, it seems probable that the invasion of the *Pfrille* by *Thelohanellus* had taken place after that by *Myxosoma*.

Morphology

Very few stages other than spores were present, and they had no special peculiarities. The spores, which were normal and uncalcified, showed considerable range in dimensions, being 11·4–16·4 μ long and 7·3–10 μ broad. Most of the spores are oval in contour (Figs. 4–6), while others may be somewhat ovoid (Figs. 1–3), which may be due to earlier mutual pressure or to contact with calcified spores. The valves are relatively thin, transparent and without markings. The parietal nuclei (Figs. 5, 6) may be one or two in number, and at first are oval bodies but become compact and ultimately disappear. The sutural ridge is indistinct.

The polar capsules are pyriform, 4·1–5·5 μ long, but exceptionally are up to 7·3 μ in length, and 2·3–3·2 μ broad, the latter breadth not being common. The capsulogenous nuclei vary from biconvex in outline (Fig. 4) to curved, almost linear masses (Figs. 2, 3) capping the polar capsules and eventually becoming dot-like masses (Fig. 6), which ultimately disappear.

The sporoplasm is homogeneous. The sporoplasmic nuclei vary in size and position, the majority being small nuclei (Figs. 1–4), though occasionally a large spore with nuclei larger than the average is observed (Fig. 6).

Systematic position

The *Myxosoma* here described has been compared with other species of *Myxosoma* from Canadian fresh-water fishes. From the Ulverton River itself another *Pfrille neogaeus* infested with *Myxosoma pfrille* has been found. This second *Myxosoma* from *Pfrille neogaeus* taken from the Ulverton River feeder is not the same organism, for *Myxosoma pfrille* has spores with well-marked thickenings or foldings on their valves and none such have been seen in the *Myxosoma* under discussion. Also, the sporoplasmic nuclei of the present form are usually much smaller and have much less chromatin deposited on their nuclear membranes. It is possible that it may be the same as *M. ellipticoides*

from *Catostomus commersonii*, but the presence of large, conspicuous parietal nuclei is a noticeable feature of *Myxosoma ellipticoides* and is not so in the present form. Its nearest affinity appears to be with *M. ellipticoides*, but there are differences as indicated. It seems best, with the information at present available, to consider it provisionally as a new species and it is, therefore, designated *M. parellipticoides* n.sp., with characters as outlined.

Myxosoma catostomi Kudo

(Pl. IV, figs. 7–21)

Among a collection of *Catostomus commersonii* taken from a feeder of the Francoeur Brook, Nicolet watershed, were some young fish in which one to five small cysts were present. One of these, a fish 4·7 cm. long, had four small elongate cysts which were situated in individual muscles and could be seen through the skin as small whitish patches. These cysts were caused by Myxosporidia, one cyst being due to *Myxosoma* and the remaining three to *Thelohanellus*. The *Myxosoma* is provisionally considered to be a variety of *M. catostomi* Kudo, 1926, which was originally described from *Catostomus commersonii* from Douglas Lake, Michigan.

Myxosoma catostomi from Canadian *Catostomus commersonii*

Morphology

Myxosoma catostomi in various stages was found in the muscles of *Catostomus commersonii*, and zonation of parasites within the muscles was present, as seen in sections (Fig. 7). Young pansporoblasts were found nearer the periphery of the cyst within the muscle, while towards the centre multinucleate forms and spores were present.

Young sporoblasts are rounded to oval bodies, varying considerably in size. The smallest uninucleate forms observed are 2·8 by 1·4 μ, and the largest ones about 10·4 by 7·3 μ. They have finely granular homogeneous cytoplasm and nuclei with usually four thickenings on their nuclear membranes. Forms with the nucleus dividing into two have been seen (Fig. 9). Binucleate forms (Figs. 10–12) vary much in size and shape, the latter being partly determined by the space available for development. Multinucleate forms (Figs. 13, 14) are fairly numerous. The sporoblasts appear to be disporous. During spore formation extrusion of some chromatin appears to take place, as described by Kudo.

The spores of the Canadian variety of *Myxosoma catostomi* (Figs. 15–21) are ovoid to almost rounded, ovoid forms being the common type. They are 10–12·7 μ long and 7·6–10 μ broad. The range is thus smaller than that given by Kudo, which is 13–15 μ by 10–11·5 μ. The sporocyst of the Canadian form shows a series of folds or thickenings, though they have not the regularity of number—six to eight—described by Kudo, nor can the thickenings or folds be described as triangular. In some spores they do not show. The sutural

ridge (Fig. 21) is very slightly curved and the two valves are not quite the same size. Parietal nuclei are small oval bodies.

The polar capsules are pyriform and are 3·6–5·5 μ long and 1·3–2·7 μ broad. The capsulogenous nuclei are small oval karyosomatic bodies (Fig. 21), which become narrower and oval (Fig. 20), then rod-like (Figs. 16, 18) and finally disappear. The polar filaments are not easily discernible in our material. A few spores showed fine filaments of several coils. Extruded polar filaments have not been observed.

The sporoplasmic nuclei are small, rounded, with chromatin in the karyosomes and deposited on the nuclear membranes. The two nuclei are generally arranged transversely parallel to one another.

Systematic position

This *Myxosoma* from Canadian *Catostomus commersonii* is considered to be a small race or strain or variety of *Myxosoma catostomi* Kudo. The main features of its different stages agree with those given by Kudo; there are, naturally, different lengths of polar capsules corresponding with different ranges of spore dimensions. Its localization in muscles of the host is the same. It appears preferable to consider this form as a race or variety, the differences being insufficient to justify the creation of a new species.

Family MYXOBOLIDAE

The Myxobolidae is the largest family of the Myxosporidia. Representatives of three of the genera of the Myxobolidae have been found in fresh-water fishes in the Province of Quebec. They include members of the genera *Myxobolus*, *Thelohanellus* and *Henneguya*. A number of species of Myxobolidae new to science have been under observation and new hosts for Myxosporidia are recorded.

Myxobolus

Species of *Myxobolus* are herein described from eleven different piscine hosts in Quebec Province.

Myxobolus poecilichthidis n.sp.

(Pl. V, figs. 1–14)

Among a collection of darters, *Poecilichthys exilis*, from Black Lake in the Becancoeur watershed, was a specimen with four creamy cysts, about 0·5 mm. in diameter, situated in fatty connective tissue attached to the gut. These cysts were due to a species of *Myxobolus* with delicate-looking, narrow, oval to ovoidal spores. As far as can be ascertained, *Poecilichthys exilis* is a new host for *Myxobolus*.

Morphology

The cysts containing *Myxobolus* from *Poecilichthys exilis*, unfortunately, were in an advanced stage of development, spores and amoebulae only being found.

The amoebula (Fig. 1) has an irregularly shaped outline owing to the presence of relatively long ectoplasmic pseudopodia. The body may be up to 7·6 μ in diameter exclusive of the pseudopodia. The cytoplasm is granular. Two round nuclei, each with a distinct uniform nuclear membrane, and well-marked karyosome, are present.

The spores (Figs. 2–14) are delicate in appearance. They are fairly uniform and vary from oval to narrow ovoid in outline, being 12·3–15·4 μ long and 4·5–6·8 μ broad. They are somewhat narrower from the sutural plane aspect. Many are from 5·5–6·4 μ broad. The valves are smooth, unthickened and relatively thin. The sutural ridge (Figs. 6, 10, 11, 13) is almost straight or but slightly curved. The valvular nuclei may be oval (Figs. 8, 9, 13) or compact (Fig. 2). In many spores they had disappeared. They are usually situated at the posterior or non-capsular end of the spore, but occasionally some have been seen half-way down the spore.

The polar capsules are elongate-pyriform structures, sometimes equal (Figs. 4, 9, 12, 13) and sometimes unequal (Figs. 2, 6, 8) in length. They are 5–7·3 μ long and 0·9–2·3 μ broad. The capsulogenous nuclei are on or near the rounded ends of the capsules, and, when karyosomatic, may be almost as large as the sporoplasmic nuclei (Figs. 8, 11, 12). In some (Figs. 3, 6) one capsulogenous nucleus may have disappeared; in others (Fig. 9) neither can be seen. The polar filaments form a series of somewhat loose folds (Figs. 6, 7, 9, 11, 13) within the capsules. Partly extruded filaments (Fig. 14) only have been observed, these being up to 35 μ in length.

The sporoplasm may form a fairly compact mass, but in some spores clear processes or pseudopodia have been seen (as in the amoebulae), extending between the polar capsules and between the polar capsules and the valves. The sporoplasmic nuclei are small and rounded, with well-marked karyosomes and distinct unthickened nuclear membranes. In many spores they are arranged tandem (Figs. 4–12); occasionally they are transversely parallel (Fig. 3). The iodinophilous vacuole is rounded to oval (Figs. 7, 9), and varies somewhat in position and size.

Systematic position

It has been a matter of some difficulty to determine whether the *Myxobolus* from *Poecilichthys exilis* were a new species or not. Hitherto this fish has not been known to harbour Myxosporidia. The spore of *Myxobolus ellipsoides* Thélohan, 1892 has much the same range of length, but its breadth is considerably greater, being 9–11 μ. Also, its polar capsules are stated to be 4 μ long, while those of *Poecilichthys* are 5–7 μ long and 0·9–2·3 μ broad. The shape of the spore also is different, judging from Thélohan's figures 112, 114 and the dimensions. *Myxobolus angustus* Kudo, 1934 from *Cliola vigilax* in Illinois has spores 14–15 μ long and 7–8 μ broad, but its polar capsules are proportionately larger, being 8–9·5 μ, so that the two organisms show considerable differences. The parasite of *Poecilichthys* cannot be assimilated with other species of

Myxobolus, from which it is sharply separated by its width and elongated narrow polar capsules. It is, therefore, considered to be a new species and is named *Myxobolus poecilichthidis* n.sp., with characters as herein set forth.

Myxobolus dentium n.sp.
(Pl. V, figs. 15–32)

A very interesting find was that of a species of *Myxobolus* from the head of an 18 lb. muskellunge, *Esox maskinongy*, caught at Lake St Louis. The specimen was kindly sent to one of us, by a member of the Angler's Association of Quebec, as an example of "sore mouth" in this fish. On examination an infection of the palatine area by a species of *Myxobolus* was found, creamy cysts, each about 7·5 mm. in diameter, being present in and about the bases of the palatine teeth. In the infected area these teeth were loosened and readily detachable, some having already fallen out. The fisherman's stories of "sore mouth" and "fish with toothache" seem confirmed in the present instance.

Morphology

Both smears and sections of the contents of the cysts at the bases of the palatine teeth showed numerous stages of the *Myxobolus*.

The binucleate amoebulae (Figs. 15, 16) vary somewhat in shape, some being rounded, others with hints of pseudopodia. There are sometimes granules of extranuclear chromatin present (Fig. 16).

Uninucleate pansporoblasts are small rounded bodies, lying near to the periphery of the cyst. Their cytoplasm is finely reticulate. The nuclei have karyosomes and some chromatin thickenings on the nuclear membranes. Binucleate pansporoblasts with paler nuclei, perhaps about to divide, have been observed. Those measured are 7·3–11 μ in diameter. Multinucleate pansporoblasts (Figs. 18–20), with nuclei and cytoplasm in various stages of segregation to form disporous sporoblasts, have been observed. In these the cytoplasm is finely reticulate and delicate in appearance. Some indications of nuclear differentiation are seen (Figs. 18, 20). The future sporoplasmic nuclei have more chromatin than the future parietal nuclei, while the capsulogenous nuclei are slightly smaller than the sporoplasmic nuclei. Sporoblasts containing two well-formed spores (Fig. 23) are, like other stages of the parasite, frail and delicate looking. The two spores are usually parallel to one another. One or two residual nuclei may be present. In sections, sporoblasts showing valvular, capsulogenous and sporoplasmic nuclei, and polar capsules in various stages of differentiation have been seen (Fig. 23).

The spores (Figs. 24–32) are elongate-oval bodies, 11·8–14·5 μ long and 5·5–7·3 μ broad. Spores 13·2 by 6·4 μ are fairly common. The valves of the spore are thin and delicate, without any markings. The sutural ridge is straight or very slightly curved (Figs. 25, 28). The valvular or parietal nuclei may be two in number (Figs. 24, 29) or one large nucleus may be present (Fig. 26). They

are usually near the non-capsular end of the spore but they may be part way down its length (Fig. 30).

The polar capsules are elongate-pyriform. They are 4·5–7·3 μ long and 1·3–3·2 μ broad. Polar capsules with extreme dimensions are not usual. The capsulogenous nuclei are often situated on the capsules (Figs. 23–26), sometimes near the broad ends of the capsules, sometimes part way down their lengths (Figs. 24–26). The polar filament forms a series of fine loops within the polar capsule (Figs. 27, 29). A fair number of almost completely extruded polar filaments have been seen, and in some cases the filaments from adjacent spores had become entangled (Fig. 32). Such almost completely extruded polar filaments reach 70 μ long.

The sporoplasm forms a fairly compact mass around the sporoplasmic nuclei, with tenuous portions bounding the iodinophilous vacuole and sometimes extending between and around the polar capsules. The sporoplasmic nuclei are small, distinct usually karyosomatic and often with chromatin deposited as four small thickenings on the nuclear membranes. Their position in the spore varies from parallel and transverse (Figs. 26, 27) to oblique (Figs. 24, 30) and tandem (Fig. 31). Two spores within one sporoblast may have different groupings of their sporoplasmic nuclei (Fig. 23). The spores, like other stages of the organism, have a delicate, somewhat frail appearance.

Systematic position

The *Myxobolus* of *Esox maskinongy* (the muskellunge of Quebec) obviously belongs to the group of *Myxobolus* with somewhat narrow spores and elongate polar capsules. Its dimensional range is much the same as that of *M. poecilichthidis* herein described, but there are differences that enable the two organisms to be separated. On the whole, the parasite of *Esox* is more delicate in appearance than that of *Poecilichthys*. The finely reticulate or alveolar cytoplasm of the *Myxobolus* of *Esox maskinongy* has seldom been observed by us in other species of *Myxobolus* from Canadian fish. As a general statement, the polar capsules of the *Esox* parasite are broader than those of *Myxobolus poecilichthidis* and they have not the pointed extremities usual in that species. The present species is distinct from the species of *Myxobolus* described from *Esox lucius* in Europe. It can be differentiated from *Myxobolus aureatus* Ward by the shape of the spore and the proportions of the polar capsule and absence of gilt coloration. The much smaller polar capsules distinguish it from *M. angustus* Kudo. Its nearest affinity is *M. poecilichthidis*, but it seems better, at present, to consider the two forms distinct. Also, the muskellunge is a new host and the location of the parasite in the palatine teeth is unique. Plehn mentions no tooth infection of fish. It is therefore named *M. dentium* n.sp., with characters as herein described.

Myxobolus percae n.sp.

(Pl. V, figs. 33–47)

Among some yellow perch, *Perca flavescens*, purchased in Montreal and probably caught in the St Lawrence River, one was found with small cysts at the base of the pectoral fins, one on each side. The cysts were about 1 mm. in diameter and were soft and pulpy. Both were caused by a small species of *Myxobolus*. One cyst, however, had degenerated and contained only a few spores and much debris. The other showed spores and several other stages of the parasite.

Morphology

Myxobolus percae from the yellow perch is the smallest species yet recorded from Canadian fresh-water fishes.

The uninucleate pansporoblasts are rounded and are about 4–5μ in diameter. They have small karyosomatic nuclei. Binucleate forms are larger. The pansporoblasts give rise to disporous sporoblasts. Such multinucleate forms (Figs. 33, 34) show nuclear differentiation fairly early, parietal nuclei being smaller and less chromatoid than either sporoplasmic or capsulogenous nuclei. Pansporoblasts with sporoblasts with two formed spores and residual nuclei (Fig. 35) often measure up to 16·9μ in diameter. Some may be oval. Their cytoplasm is delicate and granular, their nuclei of various sizes and karyosomatic.

The spores (Figs. 36–47) are small and are oval in outline. They are 7·3–10·4μ long and 4·1–6·8μ broad. The smallest spores such as that shown in Fig. 36 are not very common, but, morphologically, they are as perfect as the larger ones. The valves are smooth, delicate and of uniform thickness except at the straight, thickened sutural ridge (Fig. 47). Valvular or parietal nuclei are oval (Figs. 41, 42, 44). Two may be present (Figs. 42, 44) or one (Fig. 41) or both may have disappeared.

The polar capsules are well formed and occupy half or rather less than half of the spore. They are pyriform and 3·2–5·5μ long and 1·3–2·3μ broad. They are usually equal in size, but sometimes one is slightly smaller than the other (Fig. 42). There is often a small space between them (Figs. 36–42), but sometimes they are in contact (Fig. 43). The capsulogenous nuclei are rounded and karyosomatic (Figs. 39, 40, 46) or else compact (Figs. 43, 44). The polar filament forms a series of coils in the capsule (Fig. 45). Polar filaments apparently fully extruded (Fig. 38) are 26–27·3μ long.

The sporoplasm is homogeneous and the iodinophilous vacuole distinct (Figs. 37–46). Two rounded karyosomatic sporoplasmic nuclei are present, usually placed transversely and parallel to one another (Figs. 36–9, 41, 42, 45), but occasionally they are slightly oblique (Fig. 40), and sometimes spores with one sporoplasmic nucleus only have been seen (Fig. 43).

Systematic position

One noticeable feature of this *Myxobolus* from *Perca flavescens* is its small size. There are several species of *Myxobolus* also of small size and recorded mostly from fresh-water fish. Comparison with these small species has shown differences from all of them. The smallest form of which we have been able to get information appears to be *M. minutus* Nemeczek, 1911, from the gills of a species of *Leuciscus* in Austria. This has a rounded oval spore, without thickenings on its valves and is 6 μ by 4·2–5 μ. Its polar capsules are 3 by 2 μ and polar filaments are up to 70 μ long. The *Myxobolus* from Canadian yellow perch has spores exceeding those of *M. minutus* in both dimensions. The polar capsules of *M. minutus* are half the length of the spore, those of the Canadian form are usually less than half. The polar filament of *M. minutus* is nearly three times the length of that of the perch parasite. These differences are sufficient to separate the two species. Reuss (1906) has described a number of species of *Myxobolus* from fishes from the Volga, many of these having small to medium-sized spores. These include *M. volgensis* from *Lucioperca volgensis*, *Myxobolus scardinii* and *M. physophilus* from *Scardinius erythrophthalmus*, *Myxobolus macrocapsularis* from *Blicca bjorkna*, *Myxobolus sandrae* from the muscles of *Lucioperca sandra*, *Myxobolus bramae* from the gills of *Abramis abramis*, *Myxobolus cyprinicola* from the gills of *Cyprinus carpio* and *Myxobolus balleri* from the gills of *Abramis balleri*. In none of Reuss's species is there the same range of dimensions as in the *Myxobolus* of the yellow perch. Also, it cannot be identified with *M. volgensis*, *M. scardinii*, *M. sandrae*, *M. bramae* or *M. cyprinicola* as these species have spores with folds or thickenings. *M. physophilus* and *M. macrocapsulatus* have pointed ovoid spores. *M. balleri* has both longer and broader spores. A number of species mentioned by Kudo (1920) are outside the range of dimensions for the form under discussion. *M. exiguus* Thélohan from the gills of *Abramis brama* and the spleen and kidneys of *Mugil chelo* and *M. capito* has spores 8–9 μ by 6–7 μ and polar filaments 15 μ, but the spores have thickenings or folds on the valves. Parisi (1912) gives the range of sizes of spores of *Myxobolus exiguus* as 8–8·5 μ by 6–7 μ. The polar capsules are 3–4 μ, and usually six folds are present on the sutural margin. Sutural folds or thickenings on the sutural margins are also present in *M. vastus* Kudo, 1934 from *Moxostoma aureolum* and the spore shows "some seven radiating lines on the posterior margin", and the spore dimensions are of a different range. The *Myxobolus* from Canadian *Perca flavescens* occurs in a new host. It seems different from all the forms discussed. From considerations of host, dimensions and morphology of the organism, it appears best to consider the *Myxobolus* of *Perca flavescens* as a new species. It is designated *Myxobolus percae* n.sp., with characters as herein set forth.

Myxobolus rhinichthidis n.sp.
(Pl. V, figs. 48–61)

A specimen of the blacknosed dace, *Rhinichthys atronasus*, from a collection made from a tributary of the Nicolet River at Ford Village, had a myxosporidian cyst about 2 mm. long inside the skin covering the suboperculum, another between the maxilla and the eye and a third immediately behind the eye. The cyst on the suboperculum, as seen in section (Fig. 48), had a thin fibrous coat, succeeded by a hyaline zone of cytoplasm, beyond which was a layer of nuclei, large and karyosomatic, followed by other stages of the parasite. The other two cysts were older, had more fibrous tissue and consisted almost entirely of spores and debris.

Morphology

Within the cyst there was a layer of homogeneous cytoplasm, beyond which was a nucleated layer. One or two layers or zones of uninucleate pansporoblasts were present, and about two layers of binucleate pansporoblasts and the same of multinucleate forms, the centre of the cyst being occupied by spores.

The uninucleate pansporoblasts have cytoplasm that stained fairly densely. The nucleus is large, with well-marked karyosome and four chromatoid thickenings on its nuclear membrane (Fig. 49). Many are about 3·2–4·5 μ long and 2·3–4·1 μ broad, and are roughly subcircular.

Binucleate pansporoblasts (Fig. 50) are more elongate. Tetranucleate forms (Figs. 51, 52) may already show nuclear differentiation. Pansporoblasts with two spores in various stages of differentiation of nuclei and polar capsules are of different sizes and shapes; some were up to 15 μ by 6·4–10 μ. One such, showing two spores, one with sporoplasm segregated around the sporoplasmic nuclei and with polar capsules, the other with sporoplasmic nuclei, capsulogenous nuclei and polar capsules, as seen in section, are shown in Fig. 53.

The spores (Figs. 54–61) are oval in outline, and are 8·6–11·8 μ long and 5·9–8·2 μ broad. The majority show no thickenings, but in a few cases thickenings or striations of the wall are present (Figs. 58, 60). Whether thickenings are present or not, the spore structures are equally well developed, and often spores with the two types of spore wall were adjacent to one another. A similar occurrence of spores with and without folds or thickenings, occurs in *Myxobolus carassii* Klokacewa. Valvular or parietal nuclei are small (Fig. 60) and but few were detected. The sutural ridge is slightly curved and wider at the periphery.

The polar capsules are pyriform, with distinct ducts (Figs. 55, 58, 61), being 3·6–5·5 μ long and 1·8–2·7 μ broad. They are slightly less or slightly more than half the length of the spore. The capsulogenous nuclei are situated on or near the polar capsules. They may be karyosomatic (Figs. 54, 56) or compact (Fig. 58). The polar filaments form loose coils within the polar capsules (Fig. 59). Extruded filaments have not been observed.

The sporoplasm is granular. It may have a small process extending between the polar capsules (Figs. 54, 56, 60), but such is not always present. The sporoplasmic nuclei are rounded and karyosomatic and occupy different positions in different spores.

Systematic position

The same difficulty arises as regards size ranges of the spores of this *Myxobolus* from *Rhinichthys atronasus* as has occurred in connexion with *Myxobolus percae*, and the details need not be repeated. *M. vastus* Kudo, 1934 from *Moxostoma aureolum* has spores which are "oblong in front view; narrowly lenticular in side view", though the illustrations show spores of rounded oval contour. "Some seven radiating lines on the posterior margin are seen in many spores." The reverse condition obtains in the *Myxobolus* from *Rhinichthys*, where few spores show thickenings or radiating lines and these are not confined to the posterior margin, nor is there an exact number of them. The spores of the *Myxobolus* from *Rhinichthys* have rather larger ranges of dimensions than those of *Myxobolus destruens* Schuurmans-Stekhoven, 1920 from *Scardinius erythrophthalmus* in Holland. The Canadian parasite is distinctly oval in front view as opposed to the pyriform shape of *Myxobolus cycloides* Gurley, which occurs on the operculum and gills and also in the kidney of *Leuciscus rutilus*, gills of *Scardinius erythrophthalmus*, *Blicca*, *bjorkna*, *Gobio gobio*, *Abramis vimba*, *A. brama*, *Rhodeus amarus*, *Alburnus alburnus* and *Lota lota* in France and Germany and in *Leuciscus rutilus* in North America. *Myxobolus cycloides* is also a larger form according to the two series of measurements given by Cépède and by Wegener.[1] A small triangular intercapsular appendix to the spore is present in the form described by Cépède but is absent from the parasite of *Rhinichthys*. From considerations of differential diagnoses, morphology and occurrence in a new host, it is felt that it would be best provisionally to consider the *Myxobolus* from *Rhinichthys atronasus* as a distinct species and it is therefore named *Myxobolus rhinichthidis* n.sp., with characters as outlined in the foregoing.

Myxobolus notropis n.sp.
(Pl. I, fig. 6; Pl. VI, figs. 1–12)

A specimen of *Notropis heterolepis* collected from the Black River, Yamaska watershed, had a number of cysts up to 2 mm. in diameter scattered irregularly over the surface of its body, whereby the surface was raised about 0·25 mm. above the general level (Pl. I, fig. 6). The cysts were caused by a *Myxobolus*. Some were young, immature cysts, others were mature, as if successional infection had taken place.

Morphology

The cysts had an outer layer of firm fibrous connective tissue. In section, young cysts showed trophic stages of the *Myxobolus*, some with seeming

[1] Quoted by Schuurmans-Stekhoven. We regret that we have not been able to consult Wegener's original thesis.

pseudopodia, intermingled with an usually single row of nuclei with cytoplasm segregating to form young pansporoblasts. In some parts of the young cyst two rows of uninucleate pansporoblasts were present. Also, large, somewhat irregular, uninucleate and binucleate pansporoblasts were seen (Pl. VI, fig. 1). In older cysts multinucleate and disporous pansporoblasts and spores were present. Some cysts showed intermediate stages of development.

The uninucleate pansporoblasts, as indicated, vary in size and appearance. They have well-formed, rather large nuclei with distinct karyosomes (Fig. 1). Tetranucleate forms (Fig. 2) are more or less rounded. Their nuclei have chromatin masses on the nuclear membranes and some extranuclear chromatin may be present. Such forms are up to 6·4 μ in diameter. Young multinucleate parasites (Fig. 3) may show seven or eight nuclei, already presenting signs of differentiation, and older ones with fourteen to sixteen nuclei have been observed. A few disporous sporoblasts, sometimes with and sometimes without remains of the pansporoblast, have been seen (Figs. 4, 5). In these sporoblasts differentiation of polar capsules and of the different types of nuclei in the spores can be seen before there is any sign of valve differentiation.

The spores (Figs. 6–12) are broadly oval in front or surface view and lenticular in end view, with a distinct slightly curved sutural ridge (Fig. 12). A slight intercapsular appendix or process may be seen in some spores (Figs. 7, 8, 11). The spores are 11·8–13·2 μ long and 7·3–9·5 μ broad. One to several valvular or parietal nuclei are sometimes seen (Figs. 6, 7, 11).

The polar capsules are pyriform, being 4·5–6·4 μ long and 1·8–2·7 μ broad. Round karyosomatic capsulogenous nuclei may be present (Figs. 6, 10), or they may become compact (Figs. 8, 11) and in some cases have disappeared (Fig. 9).

The sporoplasm stains fairly deeply. It is homogeneous. It may form a compact mass (Figs. 6, 10), but in some spores processes radiate out towards the periphery (Figs. 7–9, 11). The iodinophilous vacuole is fairly large. The sporoplasmic nuclei may be arranged parallel and transversely (Fig. 6), but more often they are tandem (Figs. 7–10). They are karyosomatic, with practically uniform nuclear membranes.

Systematic position

As far as can be ascertained, the present is the first record of the occurrence of *Myxobolus* in *Notropis heterolepis*. This myxosporidian is certainly allied to the one found in *Notropis cornutus* from Alder Brook to be described later (Pl. VI, figs. 42–48). Its identity with a number of species of *Myxobolus* is excluded on account of considerable differences in general morphology and in sizes and shapes of the spores. It cannot be identified with a number of other species having a similar or somewhat extended range of spore dimensions, because such spores have folds or thickenings on the posterior part of the spore. Such include *M. mulleri* Bütschli, *M. pfeifferi* Thélohan, *M. volgensis* Reuss, *M. sandrae* Reuss, *M. bramae* Reuss, *M. carassii* Klokacewa, *M. ovatus*

Kudo and *M. gravidus* Kudo. Shape and morphological details exclude *M. ellipsoides* Thélohan, *M. oviformis* Thélohan, *M. oblongus* Gurley, *M. sphaeralis* Gurley, *M. cyprini* Doflein, *M. balleri* Reuss, *M. macrocapsularis* Reuss, *M. squamae* Keysselitz and *M. aureatus* Ward. It is regretted that it seems impossible to identify the *Myxobolus* from *Notropis heterolepis* with already named forms, as shown by the preceding statement. Further, the host is new. For purposes of reference and in view of the present state of knowledge, it is designated *Myxobolus notropis* n.sp., with characters as herein set forth.

Myxobolus notropis from **Notropis cornutus** from Alder Brook
(Pl. VI, figs. 42–48)

A young adult *Notropis cornutus* taken from the Alder Brook, a factor of the Yamaska River, had some rather large cysts on its belly, base of the tail and back, which caused bulging of the skin. Examination of these cysts showed the presence of a myxosporidian, which we consider to be the same as or a variety of *Myxobolus notropis* from *Notropis heterolepis*. The pansporoblasts and sporoblasts are practically identical in dimensions and morphology in the two fish. The cysts in *Notropis cornutus*, however, were somewhat older than many in *N. heterolepis*, judging from the marked predominance of spores over other stages.

The spores (Figs. 42–48) are oval in front or surface view. The sutural ridge is curved and uniform. The parietal nuclei are rounded (Fig. 42) but often have disappeared. There are no folds or thickenings on the sutural edges. The spores have a slightly smaller range of dimensions than those from *N. heterolepis*, being 10·9–13 μ long and 7·3–9·1 μ broad.

The polar capsules are pyriform. The extremely small intercapsular process seen in some of the spores of *Myxobolus notropis* from *Notropis heterolepis*, was seldom seen in spores from *N. cornutus*. Capsulogenous nuclei are usually reduced to dot-like masses of chromatin (Figs. 42, 46), though an occasional round one is seen, or a spore is found with one rounded and one compact capsulogenous nucleus (Fig. 48). The polar filament has rather loose coils (Fig. 46). The polar capsules are 4·5–5·5 μ by 1·8–2·7 μ.

The sporoplasm is granular. The iodinophilous vacuole is distinct. The sporoplasm occasionally shows processes (Fig. 44) but is more often compact. The sporoplasmic nuclei may be arranged transversely parallel (Figs. 46, 48) or slightly obliquely tandem (Figs. 42, 43) or straight one behind the other (Figs. 45, 47), some type of tandem position being the more common.

Systematic position

Parallel examinations of preparations of *Myxobolus notropis* of *Notropis heterolepis* and of the *Myxobolus* from *Notropis cornutus* from Alder Brook have forced the conviction that the two are the same species, the parasite from *N. cornutus* being a slightly smaller strain of *Myxobolus notropis*. The morpho-

logical differences, perhaps due to physiological adaptation to slightly different hosts, are considered of too little significance to justify the creation of a separate species.

Myxobolus catostomi n.sp.
(Pl. VI, figs. 13–34)

Among a collection of *Catostomus commersonii* from a tributary of the Nicolet River at Ford Village was a specimen with a small yellowish or creamy cyst, about 1 mm. in diameter, situated immediately under the epithelium of the floor of the mouth and on the tip of the basihyal bone. The mucosa was slightly elevated above the ordinary level. The cyst was caused by a species of *Myxobolus*.

Morphology

In sections it was found that the structure of the cyst is as follows: The outer wall of the cyst is composed of fibrous connective tissues. Within this, at the periphery, is a rather shallow layer of granular cytoplasm, with occasional nuclei. A layer of small uninucleate pansporoblasts, another of older and larger uninucleate pansporoblasts and several layers of multinucleate forms passes towards the middle of the cyst, but the greater part of the cyst is occupied by mature spores and towards the centre these lie in a matrix with wide alveoli or spaces. Distinct zonation of the various stages of the parasite thus occurs (Fig. 13).

The small pansporoblasts, when uninucleate, are 1·36–4·1 μ in diameter (Fig. 13). Larger uninucleate forms also occur (Fig. 15). They are round to oval, with densely granular cytoplasm and karyosomatic nuclei, which have chromatin masses on their membranes. Binucleate forms (Figs. 16, 17) are up to 8·2 μ long and 5 μ broad. Nuclear division is rapid and multinucleate forms soon appear (Figs. 18–22), some showing nuclei in stages of division (Figs. 19, 22). These multinucleate forms have a characteristic fragile appearance. Early differentiation of nuclei into sporoplasmic, capsulogenous and parietal nuclei can be observed (Figs. 18, 20) in many cases but not in all (Fig. 21). Segregation of cytoplasm to form two sporoplasmic masses can be seen early (Fig. 23), also some sporoblasts with developing polar capsules can be seen in sections (Fig. 24). The sporoblast is disporous (Fig. 25).

The spores (Figs. 26–34) are typically oval. They have fairly thick valves, without thickenings or folds. The suture is slightly curved and may have one or two lateral, somewhat thorn-like processes or barbs (Fig. 29). In some spores, but not all, there is a very small knob-like intercapsular process or appendage (Figs. 26, 27, 31, 32). Such are very small and not easy to detect. Perhaps they disappear with age. One large (Fig. 34) or two small (Fig. 33) parietal nuclei may be present. The spores are 11·8–14·5 μ long and 6·8–9·5 μ broad.

The polar capsules are pyriform and are usually about the same size, being 4·5–5·8 μ long and 1·3–3·2 μ broad. Capsulogenous nuclei may be curved

(Figs. 28, 34) or dot-like masses of chromatin (Figs. 26, 27, 31). The polar filaments (Figs. 27, 30, 34) form somewhat loose coils within the capsules. Extruded polar filaments have not been seen.

The sporoplasm forms a regular mass, with a large iodinophilous vacuole. The sporoplasmic nuclei are rounded and karyosomatic. They are often arranged tandem or slightly obliquely tandem in the sporoplasm.

Free amoebulae are binucleate (Fig. 14). They often show small processes or pseudopodia.

Systematic position

The systematic position of this *Myxobolus* is also a matter of some difficulty. *Myxobolus* has not been previously described from *Catostomus*, though Kudo has given a full account of *Myxosoma catostomi* therefrom. The range of lengths of the spores is practically that of *M. ellipsoides* Thélohan, but the more elliptical spores are mostly narrower and the range is 6·8–9·1 μ contrasted with that of *M. ellipsoides* of 9–11 μ given by Thélohan and 10–11 μ given by Wegener. Both the present form from *Catostomus commersonii* and *Myxobolus ellipsoides* have smooth spores without folds or thickenings. The spores of the parasite of *Catostomus commersonii*, however, have barbs to their sutures and some have very minute intercapsular processes, not present in *Myxobolus ellipsoides*. Its lack of foldings or thickenings excludes it from the species excluded from *M. notropis*. It is provisionally considered to be a new species and is named *M. catostomi* n.sp., with characters as herein outlined.

Myxobolus catostomi from **Catostomus commersonii** from the Nicolet River
(Pl. VI, figs. 56–62)

An interesting example of local variation is afforded by *Myxobolus catostomi* from *Catostomus commersonii* collected on another occasion from the Nicolet River itself. In this collection there was a young specimen with elongate cysts, 2 mm. long and 0·5 mm. wide, in its muscles. The musculature around the cysts was much broken up and infiltration of blood had occurred. Spores were scattered throughout the muscles and the condition was one of diffuse infiltration of the parasite. Evidently the infection was of long standing and the multiplicative activity of the parasite had almost ceased, as hardly any other stages than spores were present.

Morphology

The pansporoblasts observed (Fig. 56) are small rounded to wedge-shaped organisms, with granular cytoplasm and are usually binucleate, the nuclei having karyosomes and granules of chromatin on their nuclear membranes. Only a few multinucleate pansporoblasts were seen.

The spores (Figs. 57–62) are oval to rounded, 10–11·8 μ long and 7·7–8·1 μ broad. In most cases the sporocyst is smooth, but in a few spores slight

markings or folds were present (Fig. 60). There was no intercapsular process. The sutural ridge was not very obvious. One parietal nucleus (Figs. 57, 60) to two nuclei (Fig. 62) have been seen. The sutures have barbs.

The polar capsules are small pyriform bodies, with broad ends, 3·6–4·5 μ long and 1·8–2·5 μ broad. They are less than half the length of the spore. Capsulogenous nuclei (Figs. 61, 62) were small and often were absent. The polar filaments formed rather fine tight coils (Figs. 57, 62).

The sporoplasm forms a fairly compact mass. There is a large iodinophilous vacuole. The nuclei are somewhat variable in size and shape. Large round forms (Fig. 57) and oval nuclei (Fig. 61) are both relatively rare. Usually they are karyosomatic, with distinct granules of chromatin on their nuclear membranes (Figs. 57–59); in some there is no extra karyosomatic chromatin (Figs. 60, 61).

Systematic position

The question arises as to whether the *Myxobolus* from *Catostomus commersonii* from the Nicolet River is the same as *Myxobolus catostomi* just described. There are reasons for and against this view. The range of dimensions of the *Myxobolus* from the Nicolet River is slightly smaller than those from the host collected from a tributary of the same river at Ford Village. The polar capsules have, in general, a somewhat different appearance. The sporoplasmic nuclei of the present form have more chromatin. But less is known about the trophic and multiplicative stages of the present form than about those of *M. catostomi* from *Catostomus commersonii* from a tributary of the Nicolet River. Also, the range of sizes of the *Myxobolus* spores from the two different fish intergrade, except on the lowest limit, and, as has been frequently observed by us, the state of nutrition of the host and the amount of space available for the development of the parasite are two factors that influence dimensions and also produce slight morphological differences. We therefore consider it is best to regard the *Myxobolus* from *Catostomus commersonii* here described as a physiological variety or strain of *Myxobolus catostomi*.

Myxobolus couesii n.sp.

(Pl. I, fig. 7; Pl. VI, figs. 35–41)

Among a collection of *Couesius plumbeus* from the Missisquoi County, Quebec Province, was one with a cyst in each eye, these being situated at the postero-dorsal corner of the anterior chamber, on the iris. Each cyst was about 0·8 mm. in diameter (Pl. I, fig. 7). Examinations of these cysts showed that they were caused by a species of *Myxobolus*.

Morphology

On sectioning, the cyst has been found to have a very thin, firm, external layer with small granules and extremely large nuclei, tentatively considered to be those of hypertrophied cells of the iris, constituting reaction tissue.

Immediately in contact with these large nuclei is a fairly wide multinucleate plasmodial layer, with very numerous small nuclei. Differentiated uninuclear pansporoblasts succeed the plasmodial layer and then multinucleate forms and masses of spores, the latter not being shown in Fig. 35.

The uninucleate pansporoblasts are 1·36–4·5 μ long and 0·9–3·2 μ broad. Some binucleate forms have been seen, with karyosomatic nuclei and heavy depositions of chromatin on their nuclear membranes. Multinucleate forms (Figs. 36–38) have finely alveolar cytoplasm and nuclei with abundant chromatin (Fig. 38). Early nuclear differentiation is less marked than in some other species of *Myxobolus* herein described.

The sporoblasts are disporous. In section (Fig. 39) they show alveolar cytoplasm, segregation of sporoplasmic nuclei and various stages of development of the polar capsules.

The spores (Figs. 40, 41) are rounded oval in shape, with thick sporocysts or valves that usually show no markings. Very occasionally some folds have been observed in sections, but usually the valves are quite clear. Valvular nuclei are small oval or granular structures, usually two in number (Fig. 41), but only one may be present. The suture is relatively broad and is curved. The spores are 10·4–13·2 μ long and 7·7–9·4 μ broad.

The polar capsules are pyriform, convergent structures, 4·1–5·5 μ long and 1·4–3·2 μ broad. They are less than half the length of the spore. The capsulogenous nuclei observed have been compact, somewhat crescentic bodies (Fig. 40). The polar filaments (Fig. 41) have loose coils. Extruded polar filaments have not been observed.

The sporoplasm is fairly dense and extends around and between the polar capsules (Fig. 41). The nuclei are small.

Systematic position

As far as we can ascertain, the present is the first record of any Myxosporidian parasite from *Couesius plumbeus*. The location of the parasite is unique among Canadian Myxosporidia. The only other record that we have found of the infection of the iris of a fish with *Myxobolus* is that of the iris of *Acerina cornua*, from which Awerinzew (1913) described the large-spored *Myxobolus magnus*, the spores of which are 38–45 μ long and 32–38 μ broad, the polar capsules being 15–17 μ long. The Canadian form, obviously, is not *M. magnus*. Reuss has found *M. volgensis* in the cornea of *Lucioperca volgensis*. Its spore is broadly elliptical, has three folds on the suture posteriorly but is only up to 9·5 μ long. These features preclude identity of it with the *Myxobolus* from *Couesius plumbeus*. *Myxobolus ellipsoides* Thélohan has been found on the cornea of *Tinca tinca* in France and is unlike the Canadian form under discussion. *Myxobolus mulleri* Bütschli from the eye of *Crenilabrus melops* must be excluded as its spores are spherical or subspherical, with folds on the suture posteriorly. *Myxobolus neurobius* Schuberg & Schröder, 1906, from the nerves of *Trutta fario*, has a smaller range of dimensions of spores and larger polar

capsules. Johnstone & Woodcock (1907) have described *Myxobolus esmarkii* from the cartilage and bone of the skull capsule, the cornea of the eye and the bulbus oculi of *Gadus esmarkii*. Auerbach (1910) considers *Myxobolus esmarkii* to be a synonym of *M. aeglefini*, and Kudo (1920) also so places it. The spores of *M. aeglefini* are 10·8–11·7 μ long and 9·9–10·4 μ broad, the polar capsules being 4·5–5 μ long. Also the spores have prominent folds or thickenings on the sutural edge, which are obvious in Auerbach's illustrations and which together separate *M. aeglefini* from the *Myxobolus* of *Couesius plumbeus*. *Myxobolus mutabilis* Kudo, 1934 occurs in the eye of *Pimephales notatus*, but its spores have a ribbon band, not present in those of the *Myxobolus* of *Couesius plumbeus*. The *Myxobolus* of *Couesius*, then, cannot be assimilated with other species of *Myxobolus* from the eye and from nervous tissue. Considering species of *Myxobolus* from tissues other than the eye, Kudo (1934) had described *M. ovatus* from the integument of *Ictiobus bubalis*, the dimensions of the spore of which are much the same as those of the parasite of *Couesius plumbeus*, but it has thickenings on the posterior margin and a greater range of lengths of polar capsules. The *Myxobolus* of *Couesius plumbeus* cannot be identified with previously recorded forms, its host is new for *Myxobolus*, the site of infection is unique among Canadian fishes, and the cyst structure is different. It is, therefore, considered to be a new species and is named *M. couesii* n.sp., with characters as herein set forth.

Myxobolus hyborhynchi n.sp.

(Pl. VI, figs. 49–55)

Among a collection of *Hyborhynchus notatus* from the Francoeur Brook, Nicolet watershed, was a mature male with a small cyst, 0·4 mm. in diameter, embedded in the bone at the posterior end of the mandible. This cyst was caused by a species of *Myxobolus* with relatively long polar capsules.

Morphology

Preparations of the single small cyst were limited to smears, owing to its bony situation. Unfortunately, no trophic stages of the parasite could be detected. The cyst evidently was old and spores and debris were practically the only objects present.

Binucleate pansporoblasts were few. They are elongate, up to 10 μ by 3·6 μ, with karyosomatic nuclei and thin, unthickened nuclear membranes.

The spores (Figs. 49–55) are oval to subspherical in outline. The sporocysts or valves are smooth, rather thick, without folds or thickenings and without intercapsular processes, being 9·1–10·9 μ long by 7·3–8·6 μ broad. In some one lenticular parietal nucleus is present (Fig. 49), in others one (Fig. 50) or two (Fig. 55) oval or rounded ones have been observed.

The polar capsules are pyriform and occupy much of the spore, and are 4·1–5·9 μ long and 2·3–2·5 μ broad. The capsulogenous nuclei are rounded (Fig. 52) or oval (Fig. 53). Often there is no trace of them. The polar filaments

(Figs. 51–55) form a number of fine close coils. Fully extruded filaments have not been seen, but some spores showed extrusion of a small portion of a filament (Fig. 55).

The sporoplasm is compact, with a small iodinophilous vacuole. The sporoplasmic nuclei are small rounded to slightly oval, karyosomatic and inconspicuous.

Systematic position

The number of Myxosporidia parasitic in bone and cartilage is small. Probably the best known is the organism described by Hofer under the name of *Lentospora cerebralis*. The name was changed by Kudo in 1920 to *Myxosoma cerebralis*, when he merged the genera *Myxosoma* and *Lentospora*. The "drehkrankheit" of Salmonidae in Europe due to this parasite is well described by Plehn (1924). *Henneguya trachyura* Ward encysts in the cartilaginous fin rays of *Notropis anogenus*. *Myxobolus aeglefini* is typically a parasite of the cartilage and bone of *Gadus* spp. and is the only *Myxobolus* recorded from these tissues, as far as we can ascertain. *M. aeglefini* has a broader spore with a thick sutural edge and a number of folds on its posterior margin, which are not found in the *Myxobolus* from *Hyborhynchus notatus*. The relatively long polar capsules and finely coiled filaments separate it from *Myxobolus notropis* and *M. catostomi*. Also, it occurs in a new site and in a new host. It is, therefore, provisionally considered to be a new species and is designated *M. hyborhynchi* n.sp., with characters as herein outlined.

Myxobolus subcircularis n.sp.
(Pl. VII, figs. 1–14)

Among a collection of *Catostomus commersonii* from the Francoeur Brook, a tributary of the Nicolet River, was a fish 6·6 cm. long, with a small cyst, 1·5 mm. long and 0·5 mm. wide, embedded in the ventral muscles of the pelvic fin and another smaller one on the right side of the abdomen. These were produced by a species of *Myxobolus* with mostly spherical to subspherical spores.

Morphology

The contents of the cysts were the same in both cases, small pansporoblasts and spores being the predominant stages.

Uninucleate pansporoblasts are small rounded organisms, up to about 4·5 μ in diameter. The cytoplasm is homogeneous and finely granular. Small extranuclear granules of chromatin may be present in older uninucleate forms, indicating incipient division. The nucleus is round and karyosomatic. The binucleate forms are rounded (Fig. 3) to somewhat wedge-shaped (Figs. 2, 4, 5). Small extranuclear granules of chromatin may be present (Figs. 2–4), such probably being the karyosomes of other developing nuclei. Binucleate forms with both nuclei in different phases of division have been observed (Fig. 5).

From our material, unfortunately, we could not obtain information regarding sporoblast development.

The spores (Figs. 6–14) are typically rounded, slightly oval to spherical or subspherical, the two latter predominating, and are 9·1–11·8 μ long and 8·2–10 μ broad. The sporocyst is thin, smooth and without thickenings or folds. The suture and sutural ridge are indistinct. No intercapsular process is present. Two parietal nuclei may be present (Figs. 6, 13) or only one may be seen (Figs. 7, 8, 10, 11, 12). While they apparently persist in a number of spores, no trace of them is to be seen in others.

The polar capsules are small and pyriform, being 3·2–5 μ by 1·8–3 μ. The capsulogenous nuclei are relatively large (Fig. 12). They become small and compact (Figs. 6, 10) and finally disappear (Figs. 7, 8, 13). The polar filaments within the capsules (Figs. 8, 9, 11) do not stain well, but parts of the fine coils stain. A number of spores extruded their polar filaments and those measured vary in length from 57 to 117 μ, yet they seemed fully extruded. In some cases the polar filaments of the same spore are of different lengths.

The sporoplasm forms a compact mass (Figs. 9–12). The sporoplasmic nuclei also show variation in size but are karyosomatic, and most of them show chromatin thickenings as granules on the nuclear membranes.

Systematic position

The systematic position of this *Myxobolus* may be considered with regard to other species of *Myxobolus* having spherical to subspherical spores. Of these, *M. globosus* Gurley from *Erimyzon sucetta oblonga* (=*Catostomus tuberculatus* of other authors) has spores only 7–8 μ by 6–7 μ, so that they are much smaller than those of the form under discussion, also the spores of *Myxobolus globosus* have very wide sutural ridges. *M. sphaeralis* Gurley is also excluded, as its spores are 9 μ in diameter. *M. rotundus* Nemeczek, 1911, from the gills of *Abramis brama* in Austria, has spores 10 μ by 8–9 μ and polar capsules 3·8–5 μ, so that the parasite of *Catostomus commersonii* may be near to it, but the polar filament of *Myxobolus rotundus* is only 40 μ long, whereas that of the Canadian form may be 117 μ. A species of *Myxobolus* recorded by Southwell from *Rasbora daniconicus* in India is much larger, being 13 μ in diameter. *Myxobolus squamosus* Kudo, 1934 is 8–9 μ in diameter and consequently is outside the range. *M. teres* Kudo, 1934, from the body musculature of *Notropis whipplii*, has spores 9·5–11 μ long and 9–10·5 μ broad and *Myxobolus nodosus* Kudo, 1934, from the integument of *Pimephales notatus*, has spores 9–10·5 μ by 8·5–9 μ, so that both these species may be near, so far as dimensions of spores are concerned. But the spore of *Myxobolus teres* has five prominent oblong thickenings and a conspicuous sutural ridge, and the spore of *M. nodosus* has numerous rounded thickenings on the posterior fourth of the spore. The Canadian form has no such ornamentations. The same difference occurs in the spores of *M. congesticus* Kudo, 1934. As this *Myxobolus* from *Catostomus commersonii* cannot be identified with other members of its group on account

of morphological differences, it is considered to be a species hitherto undescribed and is named *Myxobolus subcircularis* n.sp., with characters as here outlined.

Myxobolus transversalis n.sp.

(Pl. VII, figs. 15–21)

Among a collection of *Notropis cornutus* from the Rivière des Rosières, was a specimen with five cysts, all myxosporidian in character. Four of the cysts were due to *Thelohanellus notatus*. One cyst, situated below the skin in the muscles of the side of the peduncle, contained a small *Myxobolus* with oval spores, of which the greatest diameter was across the width.

Morphology

On examination, the *Myxobolus* cyst was found to be an old one. Apart from a very few disporous pansporoblasts, spores and debris composed the greater part of the cyst.

The oval to rounded multinucleate pansporoblasts are up to 24 μ in diameter.

The spores (Figs. 15–21) are typically transversely oval in outline. They have smooth sporocysts, without foldings or markings on the rather feeble slightly curved sutural ridge. Very occasionally a hint of an intercapsular process was present (Fig. 20), but such was quite exceptional. The valvular nuclei may be rounded and karyosomatic (Fig. 19) or more compact and oval (Figs. 17, 21). The spores are wider than they are long, and are from 7·7–10 μ long and 9·1–10·5 μ broad.

The polar capsules are pyriform to conical in outline. Sometimes they are subequal (Fig. 19). They are 4·1–5 μ long and 2·3–3·2 μ broad. The capsulogenous nuclei may be rounded (Fig. 17) or thread-like (Fig. 16) or dot-like (Figs. 18, 19). Polar filaments form fine coils within the capsules (Figs. 18, 20). Extruded polar filaments have not been observed.

The sporoplasm is homogeneous. The sporoplasmic nuclei are small, rounded to oval, karyosomatic, with rather dense nuclear membranes. The iodinophilous vacuole is distinct and varies in size and position.

Systematic position

Very few spores of *Myxobolus* with transversely oval spores appear to have been recorded. *M. transovalis* Gurley, 1893 seems to be the first to be described. This occurred beneath the scales of *Phoxinus funduloides* Girard from a tributary of the Potomac River, Vermont. The spores are elliptical, 6–7 μ long and 8 μ broad, with a narrow sutural edge. In contrast the Canadian form is larger and has an indistinct suture. *Myxobolus osburni* Herrick, 1936, from the mesenteries and peritoneum of the small mouth black bass, *Micropterus dolomieu*, and the common sunfish, *Eupomotis gibbosus*, both from Lake Erie, has transversely oval spores, 9·6–11·3 μ by 9·6–12·8 μ, but these have about

ten equal folds on the sutural edge. The polar capsules are 4·8–5·6 μ long. The Canadian *Myxobolus* lacks the marked sutural ridges or thickenings of the spore of *M. osburni*, which also has a coarse polar filament of six to seven coils, compared with the delicate polar filament of many coils of that of *Notropis cornutus*. The *Myxobolus* from *Notropis cornutus* is considered to be a new species and is named *Myxobolus transversalis* n.sp., with characters as outlined here.

Myxobolus conspicuus Kudo, 1929
(Pl. VII, figs. 22–37)

Among a collection of *Moxostoma aureolum* from the St Lawrence River at Boucherville, there was one having a small, opaque, creamy cyst, 1 mm. in diameter, just below the skin on the cheek. This pinhead cyst was found to be due to a small *Myxobolus*, the spores of which had many folds on their sutural edges.

Morphology

The contents of the small cyst consisted of a number of young pansporoblasts which formed a small zone of a few layers next to the cyst wall, extremely few multinucleate pansporoblasts and sporoblasts and a large number of spores.

The uninucleate pansporoblasts (Fig. 22) are rounded to oval, with somewhat dense cytoplasm. Their nuclei are karyosomatic, without thickenings on the nuclear membranes. They may reach 5·9 μ in diameter. Binucleate forms are rounded (Fig. 23) or elongate (Fig. 24), and an increase in the amount of chromatin on their nuclear membranes occurs. Stages with three or more nuclei may be of various shapes (Figs. 25, 26). Pansporoblasts with two spores in process of differentiation were few in number in our material.

The spores (Figs. 27–37) are uniformly oval in surface view. They usually have prominent markings or folds around the sutural edge which take up stains intensely, though some spores do not show these folds (Figs. 33, 36, 37). There is no intercapsular process. The suture (Figs. 34, 35) is uniform and slightly curved. The parietal nuclei may be relatively large and oval (Fig. 36) or small and curved (Fig. 37) or granule-like (Fig. 33). They eventually disappear. The spores are 9·1–11·8 μ long and 5·9–8·2 μ broad.

The polar capsules are pyriform and their apertures are separated from one another, being 3·3–4·5 μ long and 1·3–2·3 μ broad. Capsulogenous nuclei are rounded (Figs. 32, 33), or compact and granule-like (Fig. 29) or curved (Fig. 37). The polar filaments (Figs. 28, 31, 36) form up to ten coils within the capsules. Discharged polar filaments have not been observed.

The sporoplasm is granular and stains deeply. The sporoplasmic nuclei are small.

Systematic position

Several species of *Myxobolus* have been described from members of the genus *Moxostoma*. Kudo (1934) has described *Myxobolus vastus* from *Moxo-*

stoma aureolum from Fox River, Illinois. As in the Canadian fish, there were many spores and comparatively few other stages. The dimensions of the spores given by Kudo are: length 9·5–10·5 μ, width 7·5–8 μ, thickness 4–4·5 μ, polar capsules 4·5–5·5 μ by 1·3–2·5 μ. In many spores seven radiating lines occur on the posterior margin. The sutural ridge is somewhat thickened but the line is indistinct. The *Myxobolus* from Canadian *Moxostoma aureolum* has a different range of dimensions and many more folds or radiations all round the margin. *Myxobolus conspicuus* Kudo, 1929, from *Moxostoma breviceps* from Illinois, has very much the same dimensions as the *Myxobolus* from Canadian *Moxostoma aureolum*. Like *Myxobolus conspicuus*, the sporoplasmic nuclei are small deep-staining bodies that show but little differentiation. The number of folds on the sutural edge is much larger in the Canadian form than in *M. conspicuus*, but this does not seem sufficient to constitute a specific difference. The *Myxobolus* from *Moxostoma aureolum* from Quebec Province is, consequently, considered to be a race or strain of *Myxobolus conspicuus*. It seems probable that the distinctions between *M. conspicuus* and *M. vastus* may be found to be insufficient for recognition as two species. In that case, *M. conspicuus* has priority and *M. vastus* would pass into synonymy. The present record extends the number of hosts and the geographical distribution of *Myxobolus conspicuus* far to the east on the American Continent.

Myxobolus grandis n.sp.

(Pl. I, fig. 2; Pl. VII, figs. 38–53)

Some young *Notropis cornutus*, 2·8 cm. long, taken from a tributary of the Salmon River that entered a pond at Scotstown (St Francis watershed) had large cysts visible through the wall of the abdomen. In each fish it occupied the posterior end of the abdomen and extended forward as a broad sheet to the left-hand side of the anterior end of the body cavity (Pl. I, fig. 2). On dissection, the cyst was found to be about 8 mm. long and 5 mm. wide. It was caused by a species of *Myxobolus* with large oval spores.

Morphology

The cyst had a moderately thick outer capsule of fibrous connective tissue, with darker spots due to the pigmented peritoneal tissue of the host. Within was a narrow zone of clear cytoplasm, followed by a zone of nuclei and uninucleate pansporoblasts, then a small zone with sparse multinucleate pansporoblasts and sporoblasts, the bulk of the cyst being filled with numerous spores.

The uninucleate pansporoblasts (Fig. 38) are rounded to oval, with granular cytoplasm and large, conspicuous karyosomatic nuclei and distinct, usually unthickened, nuclear membranes. They measure up to 4·5 μ in diameter. Binucleate pansporoblasts (Figs. 39, 40) may be slightly lobed or rounded. In some (Fig. 39) there are depositions of a few small chromatin granules on the nuclear membranes; in others there are none. Multinucleate forms (Fig. 42) have nuclei in various stages of division. They may be somewhat irregular in

shape due to mutual pressure and pressure from the adjacent layers of spores. Such pansporoblasts and sporoblasts were relatively few in our preparations. In sections differentiation into two spores could be seen, some late stages showing well-developed capsulogenous nuclei and polar capsules, with segregation of sporoplasm around the sporoplasmic nuclei (Fig. 43).

The spores (Figs. 44–53) are mostly broadly oval in outline, though occasionally one may appear ovoid (Fig. 50), and are 13·2–17·3 μ long and 9·5–10·9 μ broad. Extremely few spores 13·2 μ in length were found, the usual range began at about 14·5 μ. The sporocyst is relatively thick, is smooth, and has no folds or intercapsular process. The sutural ridge is rather thick and some show a few slightly oblique or transverse barbs passing outwards from the ridge, the said barbs staining fairly heavily with iron haematoxylin. The valvular nuclei are large oval bodies, two (Fig. 49) or one (Figs. 44, 48, 51, 52) being present. They gradually decrease in size (Figs. 50, 53) and finally disappear, but they appear to persist for a long time.

The polar capsules are relatively small compared with the spore, being 4·5–6·4 μ long and 2·3–3·6 μ broad. Some show distinct ducts (Figs. 45, 48, 53). The capsulogenous nuclei observed were occasionally small, rounded and karyosomatic (Fig. 48), sometimes compact (Figs. 50, 51), and sometimes both types were present in the same spore (Fig. 49), the capsulogenous nuclei thus showing unequal gradients of development and absorption. The polar filaments (Figs. 48–53) form somewhat loose and irregular coils within the capsules. Fully extruded filaments have not been observed, but some partly extruded ones (Figs. 52, 53) were up to 30 μ long.

The sporoplasm forms a compact mass, with a relatively small iodinophilous vacuole. The sporoplasmic nuclei are usually large, rounded to oval or conical bodies (Figs. 44–53), sometimes with excentric karyosomes (Figs. 45, 46, 52), sometimes with approximately central ones (Fig. 49). Some spores with small nuclei have been observed (Figs. 46, 49), but they were relatively few in number. Subequal sporoplasmic nuclei (Fig. 48) are also sometimes present.

Some free amoebulae have been observed (Fig. 41). These often have two blunt, clear pseudopodia and are binucleate, the nuclei usually being equal in size but sometimes unequal (Fig. 41). Such occurrences might be interpreted as sexual phenomena, but the vexed question of sexuality in the Myxosporidia is not being discussed in the present paper.

Systematic position

This *Myxobolus* from *Notropis cornutus* from the Salmon River is the largest one with oval spores to be recorded both from this host and from Canadian fresh-water fishes. The nearest *Myxobolus* in size recorded from the American Continent appears to be *M. associatus* Nemeczek, 1926, from the kidney of *Leporhinus mormyrops* in Brazil. This has oval spores 15 by 10 μ, with polar capsules 7 μ long. The spore of *Myxobolus associatus* has a more pointed anterior end and approximates from oval to broad pyriform in appearance,

judging from the illustrations. Also, it has folds on the suture in some cases. The Canadian *Myxobolus* has no folds. *M. gravidus* Kudo, 1934 and *M. compressus* Kudo, 1934 have spores 12–14 μ by 9·5–10 μ and 12–14 μ by 7–10 μ respectively, and both are ovoid to elliptical. Both have markings along the posterior margin, so cannot be identified with the parasite under discussion. The much larger polar capsules and narrower spores presenting an elongate-pyriform side view exclude *M. koi* Kudo from Japanese *Cyprinus carpio*. The dimensions of spores of *Myxobolus cyprini* Doflein, 1898, *M. permagnus* Wegener, 1910 and *M. gigas* Auerbach, 1910 are too great, as well as other differences existing. From all considerations, it is necessary to create a new species for this *Myxobolus* from *Notropis cornutus*, and it is named *Myxobolus grandis* n.sp., with characters as herein set forth.

Myxobolus ovoidalis Fantham, 1930
(Pl. VII, figs. 54–65)

An 18 oz. speckled trout, *Salvelinus fontinalis*, from a private stream in the Laurentians, was brought to two of us by the owner when we were his guests. A small cyst was present at the angle of one pectoral fin. This cyst was sub-epidermal and, when removed, was pulpy. On puncturing the cyst, fluid immediately spurted out. It was found to contain much debris and various developmental stages and spores of a *Myxobolus* that at once recalled *M. ovoidalis* described by one of us from South African barbel and carp. Subsequent more detailed examination and comparison with preparations of *M. ovoidalis* showed no point of difference between the two organisms. Morphologically they were indistinguishable.

Morphology

The young pansporoblasts are rounded. Many of them are 9–15 μ in diameter and have finely granular cytoplasm. The nucleus of the pansporoblast has a small, more or less central karyosome and usually four chromatin thickenings on its nuclear membrane. Binucleate pansporoblasts (Fig. 34) showed similar nuclear structure. Some reached 25 μ in diameter. Each pansporoblast formed two sporoblastic areas, each of which gave rise ultimately to one spore. Multinucleate forms (Fig. 55) with two sporoblastic areas already show differentiation of nuclei, narrow nuclei being the forerunners of the parietal nuclei of the spores. Pansporoblasts with two fully formed spores and residual nuclei (Fig. 56) are rounded to ovoidal. The pyriform to ovoid spores are often separated from one another, the broad end of one lying in the opposite direction to the other.

The spores (Figs. 57–65) are elongate-oval to pear-shaped bodies, which in fresh preparations, are nearly 18–26 μ long and 8–15 μ broad (the limit 15 μ being rare) and up to 9·1 μ in thickness. A few slightly smaller spores have been found, as in *M. ovoidalis* from South African fresh-water fish, but the usual dimensions are as given. The valves are thin and without thickenings. Both

sutural ridge and line are indistinct. The valvular nuclei may be rounded (Figs. 61, 64) or oval (Figs. 56, 58, 59), elongate linear (Fig. 62) or dot-like (Fig. 57). Sometimes one only has been observed (Fig. 58).

The polar capsules are elongate-pyriform and often are somewhat unequal in size (Figs. 57, 61, 62, 64). Larger polar capsules are 9·5–14 μ, the latter length being relatively rare, and the smaller ones 8·2–11·8 μ. The capsulogenous nuclei are small and round (Figs. 57, 60–64) or dot-like (Fig. 59). Polar filaments (Figs. 58, 59) show as spirally coiled threads within the capsules when suitably stained. Fully extruded polar filaments could not be observed nor could extrusion be induced, but partly extruded filaments have been fairly often seen (Fig. 65). In the case of polar filaments of *M. ovoidalis* from South African barbel and carp, the polar filaments have reached 75 μ in length.

The sporoplasm is granular. The sporoplasmic nuclei are distinct, karyosomatic, with well-marked chromatin masses on the nuclear membrane and fine stainable threads sometimes connecting the karyosome to the thickenings. The iodinophilous vacuole is small and is rather more easily demonstrable than that of the South African *M. ovoidalis*.

Systematic position

Detailed comparison of all stages of the life cycle of the *Myxobolus* from the Canadian speckled trout with those of *M. ovoidalis* from South African barbel and carp has revealed practically no differences of morphology or of dimensions. The only minor difference that we have noticed is that there may be a very slightly smaller proportion of spores showing markedly asymmetrical or unequal polar capsules in the case of the parasite of the speckled trout; slight asymmetry is constant. We have no hesitation in considering that *M. ovoidalis* from South African barbel and carp and this *Myxobolus* from the Canadian speckled trout are identical.

In South Africa, barbel and carp suffer extensive injury from *M. ovoidalis*, with resultant high mortality among them. The condition, known locally as "measles" and as "pap disease", had been prevalent for many years, according to statements made to one of us who investigated the malady. Such a condition apparently has never been heard of in Quebec Province, and enquiries of various anglers, fishing clubs and Government officials has practically always met with the statement that no such infection has been met with in the speckled trout, a most popular game fish. The only exception has been the donor of the infected trout, who stated that he had seen one other case some years ago but believed it was due to the occurrence in the same water of suckers (*Catostomus*) that had "white lumps on their fins". The condition appears to be new to trout, and the suckers examined at the same time had an infection of *Thelohanellus* only, so that the hypothesis of contamination from the suckers had to be abandoned in the present case. The discontinuous distribution of *Myxobolus ovoidalis* may be considered as evidence of its spontaneous evolution

in two widely different hosts in different geographical regions or as the survival of a *Myxobolus* from a formerly much more widely distributed ancestral organism.

Thelohanellus notatus Mavor
(Pl. VIII, figs. 1–67)

As indicated earlier, a species of *Thelohanellus* has been obtained by us from four genera of Canadian fresh-water fishes which have been captured in eight different localities in Quebec Province. We have also stated that we consider that local races or varieties of this one species occur, and we now present accounts of each variety.

Thelohanellus notatus from **Notropis cornutus**, Nicolet River, at St Clothilde
(Pl. VIII, figs. 1–18)

Among a collection of *Notropis cornutus* from the Nicolet River at the lowest crossing at St Clothilde was one red-fin shiner with six cysts caused by *Thelohanellus*. One cyst was on the back on the left side of the nape. Two cysts, each about 3 mm. in diameter, and elevated above the body surface, occurred on the nape. One cyst, 2 mm. in diameter, was just below and in front of the eye. Two cysts occurred at the base of the dorsal fin on the left side, each cyst being about 4 mm. in diameter and projecting beyond the general surface for about the same distance. Smears and sections showed that all these cysts were due to the same species of *Thelohanellus*.

The cyst showed well-marked zonation of the developmental stages of the parasite, as is shown in the drawing of a small part of a section of a cyst (Fig. 3). The cyst wall is composed of layers of areolar tissue, with small, almost structureless nuclei. Beneath the fibrous layer is a layer of homogeneous cytoplasm having the appearance of ground glass. This is succeeded by three to five rows of uninucleate pansporoblasts, then up to five rows of binucleate pansporoblasts, then one or two rows of pansporoblasts forming sporoblasts, then sporoblasts containing formed spores, while at the centre of the cyst and forming the bulk of it are masses of spores. The individual cysts varied in the proportionate numbers of the different stages, but young pansporoblasts and spores were the predominant constituents of each cyst.

The uninucleate pansporoblasts are rounded bodies (Fig. 3), many young ones being 2·7–3·6 μ in diameter, though some were only 1·8 μ in diameter. They have small karyosomatic nuclei. Some forms (Fig. 1), where crowding did not occur, are much larger, as are the binucleate forms under similar conditions. Small tetranucleate forms (Fig. 4) are rounded to oval, have homogeneous cytoplasm and nuclei with karyosomes and well-marked chromatin masses deposited on their nuclear membranes. Sometimes their nuclei, even at this early stage, show morphological differentiation. Successive stages in the development of sporoblasts are shown in Figs. 6–8. The future sporo-

plasmic nuclei are larger and have more chromatin than the potential valvular or capsulogenous nuclei as a rule. Each sporoblast forms two spores (Figs. 9, 10), such forms attaining up to 20 μ in length and 12 μ in breadth.

The spores (Figs. 11–18) are pyriform, with thin valves. They are 12·7–16·4 μ long and 5–7·7 μ wide. The valvular nuclei are oval (Figs. 11, 13, 15), and usually one only has been observed in this series. Sometimes, even when the spores are within the sporoblasts, the valvular nuclei have become compact and linear (Fig. 10) or even have disappeared. The suture is straight or slightly curved (Fig. 14). Occasionally dehiscing spores (Fig. 15), split along the suture, have been found.

The polar capsule is pyriform, and in spores of this variety they are 2·7–4·1 μ broad and 5·9–7·3 μ long. They have distinct ducts (Figs. 11, 13, 17). The capsulogenous nuclei, as observed in this variety, have been compact chromatoid masses, either dot-like (Fig. 11), straight and elongate (Fig. 12) or curved parallel to the end of the polar capsule (Figs. 13, 16, 18). The polar filaments form a series of coils within the polar capsules (Figs. 11–13, 15, 16). Completely extruded polar filaments have not been observed, but almost completely extruded ones (Fig. 18) are approximately 100 μ in length.

The sporoplasm forms a compact mass of finely granular consistency, in which an iodinophilous vacuole is present in various positions (Figs. 11, 12, 16–18). The sporoplasmic nuclei may be large and prominent (Figs. 11–13) with several masses of chromatin on the nuclear membrane (Fig. 13), or they may be smaller (Figs. 15–18) and rather less conspicuous. Some investigators have considered such differences of nuclei as of possible sexual significance, but, failing observations of conjugation in living material, this occurrence is recorded and the question of significance necessarily left in abeyance.

Free amoebulae from spores have been observed. They may have one large, blunt pseudopodium or, more rarely, fine filopodia may be seen.

Thelohanellus notatus from **Notropis cornutus** from Rivière des Pins (Pl. VIII, figs. 19–24)

Another variety or race of *Thelohanellus notatus* has been observed in *Notropis cornutus* from Rivière des Pins. The host was an adult fish, 5·8 cm. long, and had two cysts. One was a large cyst on the left side of the dorsal fin and was due to *Thelohanellus*. The other cyst, situated below the epithelium of the roof of the mouth and protruding into the oral cavity, was due to *Sphaerospora notropis* described earlier.

Thelohanellus notatus from *Notropis cornutus* from Rivière des Pins has a large amoebula (Fig. 19), with blunt ectoplasmic lobopodia.

The pansporoblasts until the stage of differentiation of sporoblasts are much like those obtained from *Notropis cornutus* from St Clothilde. Their nuclei are distinct and karyosomatic but have less chromatin on their nuclear membranes. The sporoblasts are larger than those obtained from the St Clothilde specimen. Many are disporous and are about 21 μ in diameter; others are

tetrasporous (Fig. 21), are usually somewhat oval and may reach 25 μ by 19·6 μ. Segregation of sporoplasm around the sporoplasmic nuclei is shown, and capsulogenous nuclei at this stage are usually rounded or oval.

The spores of this variety of *Thelohanellus* (Figs. 22–24) are relatively uniform and are somewhat broad in proportion to length compared with other strains. They are broad pyriform and are 13·6–16·4 μ long and 5·5–9·1 μ broad. The parietal or valvular nuclei (Fig. 24) are oval.

The polar capsules are pyriform, 5·9–7·7 μ long and 2·7–3·6 μ broad. The polar filaments (Figs. 22, 23) show irregular coils. Some detached polar capsules with extruded filaments have been found, the filaments measuring up to 41 μ in length. Filaments extruded from intact spores have not been observed; perhaps they reach greater lengths. It is of interest to note that in some of the spores of *Thelohanellus notatus* from this *Notropis cornutus* a second capsulogenous nucleus has been observed (Fig. 24), the significance of which will be discussed later.

The sporoplasm and sporoplasmic nuclei present no striking differences from those already described.

Thelohanellus notatus from **Notropis cornutus** from the Nicolet River (Pl. VIII, figs. 25–31)

A specimen of *Notropis cornutus* collected from the Nicolet River had a cyst on its snout which obviously bulged out the side of the snout before the eye. This cyst was due to *Thelohanellus notatus*. The predominant stages of *T. notatus* present in this cyst were the spores, together with relatively few multinucleate pansporoblasts in stages of formation of two spores.

Multinucleate pansporoblasts were oval to wedge-shaped (Fig. 25), and differentiation into one sporoblast containing two spores was observed. Two spores arranged *tête-bêche* in the remains of the sporoblast are shown in Fig. 26.

The spores (Figs. 27–31) are pyriform, are somewhat narrow and some have pointed ends. They are 12·3–15·9 μ long and 5·5–7·5 μ broad, few spores measuring 7·7 μ in breadth having been found. The suture is straight. Valvular nuclei (Figs. 28, 29) are relatively inconspicuous; they are oval or compact.

The polar capsules are flask-like or pyriform, with well-marked ducts (Figs. 27, 28, 30). They are about half the length of the spore. The capsulogenous nuclei, when present, are compact and almost linear (Figs. 29, 31). Dense staining usually obscured details of the polar filaments, but suitable specimens showed fine closely coiled filaments. A few spores showed the beginning of extrusion of their polar filaments (Fig. 31).

The sporoplasm, while usually compact (Figs. 27–29), occasionally showed small processes (Fig. 30). An iodinophilous vacuole is present. The sporoplasmic nuclei may be arranged parallel and transverse to the long axis of the spore (Fig. 28) or, more commonly, they are arranged tandem. Very occasionally a single sporoplasmic nucleus is present (Fig. 30), but, judging from the

presence of two or more chromatoid granules in the nucleus, this may represent a stage of arrested division.

This strain of *Thelohanellus* is relatively small.

Thelohanellus notatus from **Pfrille neogaeus**, Ulverton River
(Pl. VIII, figs. 32–38)

A specimen of *Pfrille neogaeus* from the Ulverton River contained a large cyst in the abdomen, which occupied the dorsal half of the cavity posteriorly and projected anteriorly on the right side as a wing, lateral to the lobe of the liver and also as a broad solid partition between the liver and the stomach. This cyst proved to be really double, part being caused by *Myxosoma parellipticoides* and the remainder, indistinguishable from it macroscopically, by *Thelohanellus notatus*.

The cyst due to *T. notatus* contained almost solely spores of the parasites. The spores (Figs. 32–38) are pyriform, with rather pointed extremities and are 11·8–16·5 μ long and 5·9–7·3 μ broad. Valvular nuclei were not observed.

The polar capsules are conspicuous dilated bodies, sometimes causing a bulge on the spore (Fig. 32), being 6·4–8·2 μ long and 2·7–4·3 μ broad. The capsulogenous nuclei are rounded (Fig. 34) or small and rod-like (Figs. 37). The extruded polar filament has not been observed.

The sporoplasm is fine and homogeneous. The sporoplasmic nuclei are small and karyosomatic. They are often arranged tandem (Figs. 33–37), less often parallel and transverse (Figs. 32, 38).

The general impression is that of a rather pointed pyriform spore with large and conspicuous polar capsule.

Thelohanellus notatus from **Notropis cornutus** from the Rivière des Rosières and from **Catostomus commersonii** from the Coaticook River
(Pl. I, fig. 4; Pl. VIII, figs. 39–53)

Among *Notropis cornutus* obtained from the Rivière des Rosières was a specimen having five myxosporidian cysts, four of these being due to *Sphaerospora notropis* and the fifth to *Thelohanellus notatus*. The cyst of *Thelohanellus* was situated below the skin in the muscles on the side of the peduncle (Pl. I, fig. 4).

The *T. notatus* from *Catostomus commersonii*, from the Coaticook River, was from the same fish that harboured *Myxosoma ellipticoides*, and the cysts containing *Thelohanellus* were not distinguishable externally from those of *Myxosoma*. (For details of the gross pathology see *M. ellipticoides*.) The structure of the cysts and of the parasite is the same in both hosts.

The cyst containing *Thelohanellus* from *Notropis cornutus* was situated below the skin in the muscles. A fibrous capsule of connective tissue with a few large nuclei was present on its inner surface. This was succeeded by a homogeneous mass of cytoplasm, followed by a zone of cytoplasm with scattered nuclei. Several rows of young uninucleate pansporoblasts were found

in some parts of the cyst, while in others they were intermingled with binucleate and multinucleate stages (Fig. 39).

In both hosts young uninucleate pansporoblasts were 3·2–5·4 μ by 2·7–4·5 μ. They are rounded and have homogeneous cytoplasm and karyosomatic nuclei with usually four masses of chromatin deposited on the nuclear membranes (Figs. 40, 41). Older stages are polynuclear (Figs. 43, 44) and are 6·8–10·9 μ long and 5·9–8·2 μ broad. Their nuclei are rich in chromatin.

The sporoblasts are disporous. They vary in shape, some being wedge-like (Fig. 45), while others are elongate-oval (Fig. 46). The spores may lie parallel to one another (Fig. 45) or be arranged *tête-bêche* (Fig. 46).

The spores (Figs. 47–53) show variation in form and size, individual ones recalling the features of the varieties already described, being 12·3–16·4 μ long and 5·9–7·7 μ broad. Some are relatively broad forms (Figs. 47, 48, 52), others are narrower (Figs. 49, 53). Sometimes the pointed end is acute (Fig. 47), in others it is rounded (Figs. 49, 53). In some spores one large valvular nucleus is present (Fig. 48), while in others two smaller valvular nuclei can be observed (Figs. 47, 49, 53).

The polar capsules are slightly less than half the spore in length, being 5·5–8·2 μ long and 2·7–3·6 μ broad. The capsulogenous nuclei may be oval (Fig. 47) or may form compact, somewhat crescentic masses (Figs. 50, 53), or may be small granules. It is of much interest to note that vestiges of a second capsulogenous nucleus may be present (Figs. 48, 49, 53), as the unicapsular condition is considered to have been derived from a bicapsular one by degeneration. The polar filaments are fine and show as a series of coils within the polar capsules (Figs. 48, 50). Extruded polar filaments up to 53 μ long have been observed.

The sporoplasm usually forms a compact mass, but in a few spores it shows attenuate processes (Fig. 52). The sporoplasmic nuclei are relatively small and uniform in size and appearance. Some are arranged transversely (Figs. 47, 52), others are tandem (Figs. 48, 49, 53). The iodinophilous vacuole in this variety is easily seen.

Thelohanellus notatus from **Hyborhynchus notatus** from Rivière des Pins (Pl. VIII, figs. 54–66)

Among some *Hyborhynchus notatus* collected from the lowest crossing of the Rivière des Pins was one specimen with a subspherical cyst, 2 mm. in diameter, situated below the epidermis over the branchiostegal rays. It was readily detachable from the subjacent bone, to which it was in no way adherent. The cyst actually extended between the interoperculum and the last branchiostegite, at a point about half-way along them. The surface of the cyst was elevated about 1 mm. above the general level of the skin. Examination of the cyst showed that it was due to a species of *Thelohanellus*, of which the general appearance was rather more delicate than some others that we had observed.

The greater part of the cyst was occupied by young pansporoblasts and numerous spores, the former, as usual, being towards the periphery of the cyst.

The uninucleate pansporoblasts are small, rather delicate, rounded bodies, the smallest ones being 2·7–3·6 μ in diameter. Their cytoplasm is finely granular and their nuclei distinct and karyosomatic (Fig. 55). Binucleate, tetranucleate (Figs. 56, 57) and multinucleate forms (Fig. 58) are present, their nuclei showing various stages of division. The pansporoblast transforms into the sporoblast, in which segregation of the nuclei to form two spores occurs (Fig. 58). Many of such sporoblasts are somewhat irregular in shape and may reach 16 μ in diameter. Differentiation of sporoplasmic nuclei can be early observed, as they have more chromatin deposited on their nuclear membranes.

The pyriform spores (Figs. 59–66) have a somewhat fragile appearance. They are 13·5–15·9 μ long and 5·9–8·6 μ broad. The suture is straight or but slightly curved. The valvular nuclei are oval (Fig. 61) or have the form of granules (Fig. 64) before they disappear. Two valvular nuclei (Figs. 63) or only one (Fig. 66) may be present.

The polar capsules are pyriform, with distinct ducts (Fig. 61). They are rather less than half the length of the spore, being 5–8·2 μ long and 1·8–3·6 μ broad, polar capsules about 6·4 μ by 2·7 μ being fairly common. The capsulogenous nuclei may be rounded and karyosomatic (Figs. 60, 62–66), situated on or near the polar capsules, or they may appear as compact granules (Figs. 59, 61). It is a noticeable feature of this strain of *T. notatus* that a number of spores show a second capsulogenous nucleus in the form of a dense granule (Figs. 60–65). Extruded polar filaments have not been observed, but some parts of the coils are shown in Figs. 62, 64.

The sporoplasm usually forms a compact finely granular mass, occasionally with small projections (Fig. 62). The iodinophilous vacuole is obvious. The sporoplasmic nuclei are mostly small and are karyosomatic, with little chromatin attached to the nuclear membranes. Some are placed transversely (Figs. 59–62), others tandem (Figs. 65, 66).

Thelohanellus notatus from **Notropis cornutus** from Alder Brook
(Pl. VIII, fig. 67)

Among *Notropis cornutus* collected from the Alder Brook was one specimen having cysts on the belly, the base of the tail and the back, these cysts causing bulging of the skin. *Thelohanellus notatus* was present in these cysts, mostly in the spore stage, the spores being 12·7–15·4 μ long and 5–7·7 μ broad. In general morphology they resembled those already described.

As in the case of *Thelohanellus* from *Hyborhynchus notatus*, a fair number of the spores showed indications of an incipient bicapsular condition, two capsulogenous nuclei being present. In addition, a single spore was found (Fig. 67), in which not only were there two compact capsulogenous nuclei, but two well-formed polar capsules. Slight further support is lent thereby to the hypothesis of reduction of a bicapsular form in the evolution of the unicapsular

Thelohanellus. It should be mentioned that this spore with two polar capsules was found in the centre of the cyst, so that extraneous origin of it is excluded.

Systematic position

The question of the identity of the *Thelohanellus* herein described as *T. notatus* Mavor is one of some difficulty. In 1933 Kudo established the genus *Thelohanellus* for Myxobolidae having pyriform spores with a single polar capsule and an iodinophilous vacuole in the sporoplasm. *Thelohanellus* was stated to be histozoic in fresh-water fish. The type species was *T. piriformis* (Thélohan).

Myxobolus piriformis was described by Thélohan (1895) from the gills, spleen and kidneys of the tench, *Tinca tinca*; he stated that the organism was first notified by Remak (1852) and studied by Balbiani (1883–4). Thélohan gave the sizes of the spores as 16–18 μ by 7–8 μ broad, the polar filament being 30 μ long. Wegener (quoted by Kudo) gave the spores as 18 μ long and 7·5 μ broad, with polar capsules 7·5 μ by 3·5 μ. We regret that we have been unable to see Wegener's account, which was in an inaugural thesis. Gurley (1893) noted briefly *Thelohanellus* (= *Myxobolus*) *unicapsulatus* from *Labeo niloticus*. Auerbach (1909) described *Thelohanellus führmanni* from the connective tissue and mucous membrane of the mouth of *Leuciscus rutilis*, this being a narrow species, with spores 18–20 μ long and 8 μ broad, the polar capsules being 9–10 μ long. In the same year Trojan described *Thelohanellus* (= his *Myxobolus*) *oculi-leucisci* from the vitreous humour of *Leuciscus rutilus*, this being a small species, with spores 9–10 μ long and 4–4·5 μ broad. The polar capsules were 5 by 2 μ. In 1916 Mavor described *Thelohanellus* (= *Myxobolus*) *notatus* from the muscles of the tail of *Pimephales notatus* from Georgian Bay, Canada. The spore was unicapsular. It was 17–18 μ long and 7·5–8 μ broad. The polar capsules were 7 by 4 μ and the polar filaments reached 95 μ in length. Later, Kudo (1934) redescribed *Thelohanellus notatus* from *Pimephales notatus*, *Notropis cornutus*, *N. blennius* and *Cliola vigilax* from Illinois. The spores were 14–17 μ long, 7–8 μ broad and the polar capsules 6–7 μ by 3 μ. The "spores taken from cysts occurring in the four different host species are indistinguishable from one another". It will be noted that Kudo extended the range of dimensions of the spores of *Thelohanellus notatus*.

Returning to chronological sequence, in 1917 Kudo described *T. toyamai* from *Cyprinus carpio* in Japan, the spores being 15 μ by 7–8 μ and the polar capsules 7–8 μ by 3–4 μ. In 1918 Kudo described a species of *Myxobolus* (now *Thelohanellus*) from the spleen of *Perca flavescens* from Wood's Hole. The spores were 18–20 μ by 8 μ, the polar capsules being 7–9 μ by 3–6 μ. It was considered to be probably *Myxobolus piriformis* Thélohan. In 1918 an account of a giant *Thelohanellus* was given by Southwell and Prashad. The host was the Indian fish, *Labeo rohita*, from Bengal. The parasite formed cysts on the gills. The spores were 30–32 μ long and 7–8 μ broad. The polar capsules were elongate, being 22–23 μ long. The polar filament was 92–97 μ long. The parasite was

named *Myxobolus* (now *Thelohanellus*) *rohitae*. It certainly cannot be identified with European or American species. Another species of *Thelohanellus*, also occurring on the gills of *Labeo rohita*, was described by them in the same paper, the spores being 13·2–13·6 μ by 10·1–10·3 μ. The polar capsules were 4 μ long. This form was named *Myxobolus* (now *Thelohanellus*) *seni*. In 1918 Schuurmans-Stekhoven described *M. swellengrebeli* from the musculature of *Rhodeus amarus* in Holland. The spores were 12–15 μ long and 8·5 μ broad. The polar capsules were 5–6 μ long and 2–3 μ broad. Schuurmans-Stekhoven noted that some bicapsular forms were present. In 1920 Kudo revised his ideas of the form he had described in 1916 as *Myxobolus führmanni* and renamed this unicapsular form *M. misgurni*. In the literature available to us there seems to be no further reference to species of *Thelohanellus* until Kudo (1933) divided the genus *Myxobolus* into two genera, *Myxobolus* being retained for bicapsular forms and *Thelohanellus* created for the unicapsular ones. In the same paper Kudo redescribed *T. notatus* Mavor, as already noted.

From the foregoing, it is clear that the *Thelohanellus* from *Notropis cornutus* from five localities in Quebec Province and from *Pfrille neogaeus*, *Hyborhynchus notatus* and *Catostomus commersonii*, cannot be the same as the gigantic *Thelohanellus rohilae* Southwell & Prashad, nor can it be the same as the second Indian form, *T. seni*, as its polar capsules are longer. The spores of *T. oculi-leucisci* Trojan are also considerably smaller than those of the Canadian form under discussion. The spores of *T. piriformis* are 17–18 μ by 7–8 μ and its polar capsules 7·3 by 3·5 μ. The spores of *T. notatus*, as revised by Kudo, are 14–18 μ long and 7–8 μ broad, the polar capsules being 6–7 μ by 3–4 μ. The spores of *T. toyamai* are somewhat smaller but have polar capsules more than half the length of the spore, so cannot be identified with the Canadian form.

The Canadian *Thelohanellus* herein described by us appear to form a series from the dimensional aspects of the spores, these being the most constant morphological feature of the parasite. Considering the spores of *Thelohanellus* from one host, *Notropis cornutus*, from different sites, in the specimens from St Clothilde the spores are 12·7–16·5 μ long and 5·5–7·7 μ broad; from Alder Brook they are 12·7–15·4 μ by 5·5–7·3 μ; from the Nicolet River they are 12·3–15·9 μ by 5·5–7·7 μ, and from Rivière des Rosières they are 12·3–16·4 μ by 5·9–7·7 μ. The whole of them fall within the range 12·3–16·5 μ long and 5·0–7·7 μ broad. The sizes of the spores of *Thelohanellus* from *Hyborhynchus notatus* would fall within the length range, and many of them would come within the breadth limits. The spores from *Pfrille neogaeus* have a lower limit of length (11·8 μ against 12·3 μ), while their breadth is within the range. The whole of spores of the Canadian species of *Thelohanellus* that we have observed fall below the range of spore dimensions of *T. piriformis*, but are almost in the range of those of *T. notatus* Mavor obtained by combining the dimensions given by Mavor and Kudo. Minor differences in the Canadian *Thelohanellus* from the different hosts have already been indicated. It appears to us that, while they are of interest, they are not of major specific importance, but rather

afford suggestive and interesting examples of physiological adaptation. Considering the variations in range of spore dimensions—the basis of differentiation of many new species—it does not seem correct, nor is it desirable, to burden literature with yet another series of specific names. We prefer to regard the species of Thelohanellus herein described as *T. notatus* Mavor, with a series of races or varieties showing slight morphological differences that vary both with the host and with the locality.

Henneguya

The genus *Henneguya* has a number of species that may be divided into two natural groups. In the first group the spore has only one simple or undivided process, popularly termed a "tail". In the second group the spore has a double or divided caudal appendage or process, the forking occurring for part or the whole of the length of the process. During our investigations of Myxosporidia in fresh-water fishes in Quebec Province, representatives of both of these groups of *Henneguya* have been under observation.

Species of *Henneguya* with simple, undivided caudal process or prolongation have been found in *Salvelinus fontinalis*, in *Notropis cornutus* and in *N. heterolepis*.

Henneguya fontinalis n.sp.

(Pl. IX, figs. 1–8)

An interesting species of *Henneguya* has been observed in a speckled trout, *Salvelinus fontinalis*, caught in the neighbourhood of Gaspe, Quebec Province. A cyst, 1·5 mm. in diameter, was present in the axilla of one pectoral fin. This cyst was due to *Henneguya* and was composed almost entirely of spores.

Morphology

The sporoblasts of this species of *Henneguya* are more or less ovoid or rounded and are disporous (Fig. 2). Some containing formed spores are about 26 by 22 μ. Those observed were all at the same stage of development, with spores in an advanced stage and one or two residual nuclei.

The spores (Figs. 3–8) are massive and like a minute tennis racquet in appearance, being 18·2–23 μ long and 8·6–10·6 μ broad. The "body" of the spore is not always easy to delimit from the appendage. It is oval and is approximately 11·8–14·2 μ long and 8·6–10·6 μ broad. The body of the spore passes into a single or undivided "tail", which is less than the length of the body of the spore. The body of the spore is oval in contour. The sporocyst is smooth and the straight suture not very pronounced. The valvular or parietal nuclei are small and relatively inconspicuous compact masses of chromatin, situated at the beginning of the caudal process. Two such small masses are usual (Figs. 6–8), but they disappear with age.

The polar capsules are distinct, pyriform to lenticular to wedge-shaped bodies, being 5·5–7·7 μ long and 2·6–4·1 μ broad. The capsulogenous nuclei

may be rounded and karyosomatic (Figs. 5–7) or may be compact chromatin masses (Fig. 4). They occupy various positions on or adjacent to the polar capsules. The polar filaments are delicate. Completely extruded ones have not been found, but partly extruded ones (Fig. 8) measured up to 52 μ. The sporoplasmic nuclei are two in number, are small and rounded, and have a karyosome and small masses of chromatin on the nuclear membranes. They vary in position in the sporoplasm (Figs. 3–8). An iodinophilous vacuole is present but is often small.

A few amoebulae (Fig. 1) from the spores have been observed. They are somewhat quadrangular bodies, with two nuclei and fine granular endoplasm.

Systematic position

The following species of *Henneguya* have been recorded from trout and salmon. *H. nusslini* was described by Schuberg & Schröder in 1905 from the subcutaneous tissue of the dorsal fin of *Trutta fario*. The total length of the spore was 32 μ, the broad part or body being 12 μ and the breadth 8–9 μ. The polar capsules are 5 by 3 μ. But the process has two portions, and hence this Canadian form cannot be the same organism. *Henneguya salvelini* Zandt, 1923 from the fin and tail of *Salmo salvelinus* from Lake Constance, Switzerland, has spores with a body length of 10–15 μ and tail processes 25–27·5 μ, but it has two caudal processes and so cannot be the organism here described. *Henneguya salmincola* Ward from the Pacific salmon, *Oncorhynchus kisutch*, also has two caudal processes, up to 38·19 μ in length.

Exclusion of other forked-tailed species of *Henneguya* limits the field for possible identities. *H. psorospermica* Thélohan, from European pike perch, is a much larger organism, with differently shaped spores. Ward (1920) has described *H. brachyura* from *Notropis anogenus*. The Canadian form from *Salvelinus fontinalis* differs in having a greater range of dimensions of spores, longer and proportionately larger polar capsules and a decidedly short, practically straight process, not sinuous nor with a cup-like end embracing the body of the spore, as stressed by Ward. Both *Henneguya clavicauda* Kudo, 1934 and *H. crassicauda* Kudo, 1934 have differences in dimensions, the process or appendage being much longer and often banded, and the polar capsules of the Canadian form are proportionately larger. *H. gasterostei* Parisi, 1912, from the kidney of *Gasterosteus aculeatus*, has a smaller spore with a single process, but the valves have fine longitudinal striae and are asymmetric, conditions not found in the *Henneguya* from *Salvelinus fontinalis*. *Henneguya macrura* Gurley has a spore with a single process which is sometimes jointed and is always proportionately longer than in the form under discussion. *H. media* Thélohan, from the kidney of *Gasterosteus aculeatus* and *G. pungitius*, is another species with a short tail process, but the proportions of the parts of the spore are different. *Henneguya creplini* (Gurley) Labbé has an elongate spindle-shaped spore, with longer and proportionately narrower polar capsules.

The conclusion, then, is that the *Henneguya* from *Salvelinus fontinalis* from the Gaspe District of Quebec is a distinct entity. It is, therefore, considered to be a new species and is named *Henneguya fontinalis* n.sp., with characters as detailed herein.

As far as can be ascertained, the present is the first notification of the occurrence of *Henneguya* as an infection of the speckled trout in the Province of Quebec, or, indeed, in Canada.

A possible bearing on the source of infection of the speckled trout was afforded by the discovery of a variety of *H. fontinalis* in a *Notropis cornutus* and *N. heterolepis* from two different localities.

Henneguya fontinalis var. **notropis** n.var.

(Pl. IX, figs. 9–21)

Among a collection of *Notropis cornutus* from the Alder Brook, Yamaska watershed, was one having a number of cysts on its abdomen, base of the tail and the back. Two kinds of myxosporidian parasites, *Thelohanellus* and *Henneguya*, were present. In many respects the *Henneguya* strongly resembles *H. fontinalis* from the speckled trout, just described.

Morphology

Young pansporoblasts are small, rounded, with a karyosomatic nucleus and chromatin masses deposited on the nuclear membrane. Older multinucleate pansporoblasts (Fig. 9) show various stages of nuclear multiplication and differentiation into two sporoblasts. The larger pansporoblasts have well-formed spores and residual nuclei (Fig. 10). Often the two spores in the sporoblast are arranged *tête-bêche*. The cytoplasm of the sporoblast is alveolar and its nuclei are karyosomatic, with chromatin deposits on the nuclear membrane.

The spores (Figs. 11–21) have much the appearance of those of *Henneguya fontinalis*. They are broad and oval, like a tennis racquet in appearance, the spores varying in total length from 16·8 to 21·8 μ, thus being smaller than the spores of *H. fontinalis*. The body of the spore is more or less oval, 9·1–13·5 μ long and 7·3–10 μ broad. The process is short, blunt and less than the body of the spore in length. The valvular or parietal nuclei are oval and karyosomatic (Fig. 16) or more often compact (Figs. 11, 13–15). Occasional extra parietal nuclei are present (Fig. 12).

The polar capsules are pyriform and convergent. They are from 4·5–7·3 μ long and 2·3–3·6 μ broad. The capsulogenous nuclei are relatively large (Figs. 11, 13, 16, 17), and in some spores are almost as prominent as the sporoplasmic nuclei (Figs. 16, 17). In other cases they are minute granules, sometimes situated half-way down the polar capsule.

The sporoplasm is distinctly granular and there is a large iodinophilous vacuole. The sporoplasmic nuclei are like those of *H. fontinalis*.

Systematic position

From the foregoing it is evident that the *Henneguya* from *Notropis cornutus* from Alder Brook has a strong resemblance to *Henneguya fontinalis* herein described. It has a smaller range of dimensions, but in other respects presents practically identical morphology. The difference in size is a constant feature. The organism is considered to be a stable, smaller race or variety of *H. fontinalis* and is designated *H. fontinalis* var. *notropis* var. nov.

Henneguya fontinalis var. **notropis** from **Notropis heterolepis**

An extremely sparse infection with a *Henneguya* practically identical with *H. fontinalis* var. *notropis* has been observed in one *Notropis heterolepis* from the Black River. The material was too scanty to permit of detailed examination, but nothing was found to indicate that the parasite was other than *Henneguya fontinalis* var. *notropis*. A spore is shown in Fig. 22. It is possible that *H. fontinalis* may have been originally derived from an ancestral form common to *Salvelinus* and *Notropis*, which has developed into a larger form in the speckled trout.

Henneguya percae n.sp.
(Pl. IX, figs. 23–37)

Some yellow perch, *Perca flavescens*, were received by one of us from a friend who had caught them in Lake Memphremagog. One of these yellow perch had a very small white nodule, about 0·25 mm. in diameter, on a gill filament. Smears and fresh preparations were made of it and a species of *Henneguya* with noticeable polygonal spores was found. There were also some of the earlier stages of the parasite. This *Henneguya* appears to be a new species. The dimensions given are those of fresh material.

Morphology

In the fresh preparations a few small amoebulae have been seen. These have a rounded body, one surface being much more curved than the other, and the less curved surface is continued as small ectoplasmic pseudopodia (Fig. 23). Such amoebulae are usually about 5 μ long and 6·4 μ broad, exclusive of the pseudopodia. They all executed feeble movements. The ectoplasm is distinct at the pseudopodia; the endoplasm is very near the ectoplasm in the body of the amoebula. All amoebulae observed were binucleate, the nucleus being karyosomatic, with hardly any extrakaryosomatic chromatin.

Young uninucleate pansporoblasts were very scarce. The binucleate ones are oval in outline and are about 6·5 μ long and 4–4·5 μ broad. In some binucleate forms the nucleus was in process of division (Fig. 24), two elongate and sometimes four small masses of chromatin being present. Tetranucleate forms (Fig. 25) have homogeneous cytoplasm and their nuclei are karyosomatic. Some in division with dumbbell-like chromatin have been observed.

Differentiation of sporoblasts apparently is rapid. Pansporoblasts containing one or sometimes two sporoblasts (Fig. 26) in various stages of nuclear differentiation were fairly common in our preparations. The parietal nuclei are more elongate than the others. Pansporoblasts with one sporoblast containing two spores have been observed. The caudal appendage of the spore develops slowly, but some spores still within the sporoblast and having well-developed furcate appendages have been seen (Fig. 27).

The spores (Figs. 28–37) have characteristic polygonal, usually pentagonal bodies, though very occasionally pressure may result in an almost hexagonal shape (Fig. 34). The caudal process is forked into two for less than half its length. The bodies of the spores are 13·2–16·8 μ long and 9·5–12·3 μ broad. The undivided parts of the caudal process are 5·4–9·1 μ long and the rami 5–9·1 μ long. Usually the rami are rather less than half the total length of the process. The valves show no striations and the sutural ridge is indistinct. The parietal or valvular nuclei may be small, oval structures at the junction of the appendage and the body (Fig. 36), or may be small compact masses (Figs. 28, 31, 34). In many spores they cannot be detected.

The polar capsules are elongate pyriform in shape, and are 8·5–10 μ long and 2·3–3·2 μ broad, being usually rather more than half the length of the body of the spore. The capsulogenous nuclei may be relatively large, round and karyosomatic, situated on or near the broad end of the polar capsule (Figs. 28, 30, 31), compact (Fig. 35) or absent (Figs. 34, 37). The polar filaments lie in fine coils within the polar capsules (Figs. 31, 35, 36). From ten to fifteen such coils have been counted. Completely extruded filaments have not been observed, but partly extruded ones are up to 48 μ long. One such partly extruded filament is shown in Fig. 37.

The sporoplasm is granular. It has processes extending around and between the polar capsules (Figs. 31, 32, 34). An iodinophilous vacuole is present and is usually situated near the sporoplasmic nuclei. These are very distinct. Usually they are small, equal in size, karyosomatic and have very little extrakaryosomatic chromatin. Occasionally one nucleus is smaller than the other (Fig. 34). Also, occasionally a spore with larger karyosomatic nuclei, with four or five thickenings of chromatin on the nuclear membranes, has been found (Figs. 30, 31).

Systematic position

Several species of *Henneguya* have been recorded from perch. *H. psorospermica* Thélohan, 1895 occurs on the gills of *Esox lucius* and *Perca fluviatilis* in Europe. It has a spore with a simple caudal appendage and the body of the spore is oval. *Henneguya testa* (Cohn) Labbé was described from the gills of perch in Germany. Wegener (1910), in an inaugural dissertation quoted by Kudo, states that the spores are 30–40 μ by 7–8 μ, with cavity length 15–18 μ and tail length 15–25 μ. It is a much larger organism than the *Henneguya* of the Canadian yellow perch. *H. minuta* (Cohn) Labbé, from the gills and ovary

of *Perca fluviatilis*, also has larger, oval-bodied spores with simple tails. Mavor & Strasser (1916) have described *Henneguya wisconsinensis* from the urinary bladder of *Perca flavescens* from Lake Mendota, Wisconsin, U.S.A. But this parasite has ovoid bilaterally symmetrical spores with bifurcated caudal appendages, which the authors' illustrations show begin near the body of the spore. The polar capsules also are small, 3·5 μ by 2·5 μ. Kudo (1934) records that 103 yellow perch examined by him in Illinois "did not exhibit any recognizable protozoan infection". *Henneguya wenyoni* Pinto, 1928 from *Tetragonopterus* sp. in Brazil is a form with smaller spores with forked processes. None of the foregoing species have polygonal spores. The nearest affinity of the species under discussion appears to be *Henneguya wisconsinensis*, but its spores are different. Also, up to the present, we have observed no species of *Henneguya* in either the urinary or the gall bladders of yellow perch examined by us in Canada, but we have found this *Henneguya* on the gills. The parasite differs from *H. wisconsinensis* in its location, the characteristic polygonal (pentagonal) shape of its spores and in having a caudal appendage with an undivided portion for more than half its length. It is distinctive. It is considered to be a new species and is named *H. percae* n.sp., with characters as outlined herein.

Henneguya salmonis n.sp.

(Pl. X, figs. 1–6)

An interesting occurrence of *Henneguya* in the Atlantic salmon, *Salmo salar*, came to light when half a salmon bought in Montreal was being prepared for cooking. A small speck was noticed beneath the skin near the dorsal fin. On puncturing, the fluid that exuded was found to contain spores of a species of *Henneguya*. It is regretted that the organism has not been found again, so that description of the spores only is possible. The local name of the fish is Gaspe salmon, and this name is restricted to Atlantic salmon, *Salmo salar*, from the well-known salmon rivers of the Gaspe Peninsula, Quebec Province.

Morphology

The spores of *Henneguya salmonis* n.sp. from Gaspe salmon have small bodies with long caudal processes that fork near the junction of the caudal appendages with the bodies (Figs. 1–6). The body of the spore is oval in surface view (Figs. 1–4) and conical when seen with the suture in the median position (Fig. 5). The two portions of the caudal appendage may be subequal in length. They may be apposed (Figs. 1, 2) or separated (Figs. 3–6). For about half their length they are almost filamentous in appearance.

The oval body of the fresh spore is 10–11·6 μ long and 5–7·7 μ broad. The small undivided portion of the caudal process is 1·8–3·6 μ long and the forks or rami are 35–42 μ long. The valves are smooth and the sutural ridge (Fig. 5) is narrow and straight. The valvular or parietal nuclei are situated in the undivided part of the caudal process, two usually being present, either side by side (Fig. 2) or at different levels (Figs. 1, 3, 4).

The polar capsules are pyriform and are 4·5–5·5 μ long and 1·5–2·3 μ broad. The capsulogenous nuclei (Figs. 1–3) are small. Only a few extruded polar filaments have been observed (Fig. 6), and these did not appear to be fully extruded. They were up to 25 μ long.

The sporoplasm is homogeneous. The iodinophilous vacuole lies near the nuclei. The sporoplasmic nuclei are karyosomatic with four chromatin thickenings on their nuclear membranes. These nuclei are arranged parallel to one another and nearly level with the polar capsules in all the spores examined.

Systematic position

Records of the occurrence of *Henneguya* among different kinds of salmon seem rare. Ward (1920) described *H. salmincola* from the muscles of a Pacific salmon, *Oncorhynchus kisutch*, sent to him from the Stickeen River, Alaska. In connexion therewith Ward (1920, p. 63) stated: "I have not been able to find a single record of the occurrence of Myxosporidia in an adult European salmon and not one in a salmon of any age from this continent." Prof. Ward had an enormous personal experience, for over a period of fifteen years he had personally examined several thousand salmon of all species, and, with the help of voluntary assistants, had records of "several hundred thousand fish", but had found only the one case of myxosporidian infection then described, namely, *Henneguya salmincola*. The careful detailed description and drawings of Ward show that the *Henneguya* herein described from Atlantic salmon, *Salmo salar*, cannot be the same organism as *Henneguya salmincola* Ward. The dimensions of the spore are smaller than those of *H. salmincola*, the caudal process is more sharply delimited, the valvular nuclei are much smaller, the polar capsules are proportionately longer and the spore wall has no thickenings. No further records of *Henneguya* from salmon since Ward's paper appeared have been traced, so that his comment on the scarcity of Myxosporidia in salmon still holds, and we were extraordinarily fortunate in finding the present *Henneguya*. *H. salmincola* appears to be the nearest affinity to this *Henneguya* from the Atlantic salmon, but the two are distinct. There is a difference in host and very different distribution of the salmon concerned. The *Henneguya* from *Salmo salar* is a distinct entity and it is, therefore, named *Henneguya salmonis* n.sp., with characters as herein set forth.

Henneguya esocis n.sp.
(Pl. X, figs. 7–26)

A distinct species of *Henneguya* has been found on the gill filaments of one out of eight *Esox niger*, the pickerel, taken from Brome Lake. The same organism has since been observed in a pickerel from Fisher's Bay on Brome Lake. The Brome Lake pickerel weighed 2 lb. Small elongate whitish cysts occurred, each on a branchial filament. Smears and sections were made.

Morphology

Sections of cysts showed that there was an external layer of fibrous tissue with large nuclei, succeeded by a zone of homogeneous cytoplasm with scattered nuclei, then two to three rows of young pansporoblasts, while nearer the centre of the cyst were various multinucleate stages and sporoblasts, the greater part of the cyst being occupied by spores. Part of such a section showing zonation of the stages of the parasite is shown in Fig. 13.

The uninucleate pansporoblasts (Fig. 7) are subspherical, varying from 2·2 to 5·5 μ in diameter. They have distinct nuclei with small karyosomes and about four small chromatin masses on the nuclear membranes. Forms with dividing nuclei are somewhat larger (Fig. 8). A few binucleate stages, closely applied to the cyst wall, have been observed (Fig. 9). Multinucleate forms with one or more nuclei undergoing division have been seen (Fig. 10). In sections sporoblasts were found showing two relatively large sporoplasmic nuclei, two small rounded capsulogenous nuclei and two lenticular parietal nuclei, with two polar capsules differentiated (Fig. 11). Sporoblasts with polar capsules and some coils of polar filaments have also been observed (Fig. 12). In both smears and sections disporous sporoblasts of somewhat irregular shape have been found, one spore sometimes being almost at right angles to the other (Fig. 14). Such spores have their polar capsules with distinct, round, karyosomatic capsulogenous nuclei. The caudal appendages are in various stages of development.

The spores (Figs. 15–25) are very characteristic. They have long, somewhat bullet-shaped bodies, with caudal processes each about half the width of the body at its origin, passing posteriorly as a narrow triangular process and continuing as a considerably longer, thinner, filamentous part. There may be a slight constriction below the polar capsules (Figs. 18, 21, 23), so that a tadpole-like appearance results. The caudal appendages are flexible and curve over one another (Figs. 21, 22, 25, 26). The spores to the fork are 15–23·6 μ long, and 3·2–4·6 μ wide. The caudal rami are 19–50 μ long, extremes being rare. Some spores are narrow (Fig. 17), others wide (Fig. 20), but most of them are of medium width. The valves are thin. Parietal or valvular nuclei are usually densely staining chromatin masses, parallel to the long axis of the spore, near the origin of the caudal forks (Figs. 16, 17, 19, 22); occasionally a spore with oval karyosomatic parietal nuclei is seen (Figs. 22, 25).

The polar capsules are elongate-pyriform structures with distinct ducts (Figs. 23–26). They are 5–7·3 μ long and 1·4–2·7 μ broad. The capsulogenous nuclei are situated on (Figs. 17, 20) or near (Figs. 15, 16, 18) the polar capsules. They may be karyosomatic (Figs. 15–18) or reduced to small, chromatin masses (Figs. 23–25). The polar filaments (Figs. 19, 21) form a series of coils within the capsules, up to ten coils having been seen. Extruded polar filaments have not been observed.

The sporoplasm is very dense and extends into the caudal forks. Small

definite masses of densely staining chromatin are scattered through the sporoplasm. The number of these may be small (Figs. 15, 23), or relatively numerous (Figs. 20–22). No special arrangement of this extranuclear chromatin has been observed. It is a normal feature, for such occurs in spores still within the sporoblasts. They cannot be interpreted as additional parietal nuclei, as they persist long after the ordinary parietal nuclei disappear, and also, in sections, some are seen to be situated deep in the sporoplasm.

The sporoplasmic nuclei are karyosomatic, with small karyosomes and a fair amount of chromatin on their nuclear membranes. They are usually arranged tandem (Figs. 15–24). Like the sporoplasm, the sporoplasmic nuclei stain densely. A very small, often indistinct iodinophilous vacuole has been detected in some spores (Fig. 21), but it is frequently obscured in stained specimens by the densely stained cytoplasm and chromatin granules.

Systematic position

This species of *Henneguya* from *Esox niger* is unlike other species reported from the European pike, *E. lucius*. These include *Henneguya psorospermica* Thélohan, the spore of which has an undivided caudal process, *H. schizura* (Gurley) Labbé, *H. lobosa* (Cohn) Labbé and *H. peri-intestinalis* Cépède, though that author says that *H. peri-intestinalis* resembles *H. psorospermica*, with which it may be identical. Kudo (1929) has described *H. exilis* from the gills of a channel catfish, *Ictalurus punctatus*, obtained at Sterling, Illinois. *Henneguya exilis* has an elongate spore which, exclusive of the process, is 18–20 μ long and 4–5 μ broad, the total length being 60–70 μ. The polar capsules are 8–9 μ by 1–1·5 μ. Also, the spore is spindle-shaped, and the valvular processes have not first distinct wider and then filamentous parts. Kudo's illustrations (his Pl. 19, figs. 54, 55) show large distinct iodinophilous vacuoles posterior to the sporoplasmic nuclei. *H. exilis*, like the form from *Esox niger*, has extranuclear chromatin. The differences in range of dimensions, proportion of parts, bullet or tadpole shape of the spore, caudal appendages with well-marked wider and then filamentous portions and very narrow and inconspicuous iodinophilous vacuole readily separate the parasite of the pickerel from that of the channel catfish. The *Henneguya* of *Esox niger* is considered to be new to science and is named *Henneguya esocis* n.sp., with characters as herein set forth. It is believed that this is the first report of the occurrence of *Henneguya* in *Esox niger*.

EFFECTS OF THE PARASITES ON THE HOSTS

The gross macroscopic manifestations of infection of Quebec fresh-water fishes with Myxosporidia have been indicated in connexion with the various Myxosporidia described. Some general notes on such have already been published by two of us (1937). The vast majority of the parasites that we have observed are histozoic, situated in the tissues, such as the subcutaneous connective tissue, and the muscles of the hosts. More rarely they are coelozoic,

as when they fill or partly fill the abdominal cavity. But the distinction between histozoic and coelozoic Myxosporidia is not hard and fast, and an organism at first histozoic may grow and extend beyond its original site, becoming coelozoic. Thus, the histozoic myxosporidian, *Myxosoma notropis*, at first parasitic in the liver of *Notropis cornutus*, has extended beyond it and almost blocked the abdominal cavity, a large part of it then being coelozoic. Mesenteric cysts have often been of relatively large size.

The musculature of the body wall and the subcutaneous tissues, especially near the fins, are common sites of infection. Less common sites are the cheek, roof of the mouth, orbit of the eye, the nasal area, the mandibular bones and the iris. In one case of "sore mouth" in *Esox maskinongy*, there was an infection with *Myxobolus dentium* in the epidermal tissues in and about the bases of the palatine teeth, which were loosened and readily detachable, some having already fallen out. In a *Notropis cornutus* the eye was forced out laterodorsally by a cyst due to *Myxosoma orbitalis*, the suborbital ring being carried out with it. The small glistening nodules due to *Henneguya* on the gill filaments in some cases have caused considerable obstruction of the blood flow therein. In some cases of abdominal tumours, due to Myxosporidia, vascularization has occurred, as in the abdominal tumour of *Notropis cornutus* due to *Myxosoma media*.

In marine fishes two of us have described the effects of Myxosporidia on the gall bladders of marine fishes (Fantham & Porter, 1912*a*). We have observed similar effects on the gall bladders of certain marine fishes and a few fresh-water fishes in New Brunswick, Canada, but have not much information regarding such in the fishes of the Province of Quebec.

The effects on the musculature of invasion by Myxosporidia are noticeable. Intermuscular parasites cause progressive atrophy of the adjacent as well as the infected muscles. Infection of individual muscular fibres produces hypertrophy, with attenuation of sarcoplasm and nuclear deformation. Diffuse infiltration of muscles by Myxosporidia causes disintegration of the tissues, so that the muscle becomes reduced to a series of scattered fibrillae forming a meshwork filled with masses of the parasites.

Frequently tissue degeneration with pus formation occurs, and the host reacts by producing fibroblasts that ultimately form fibrous tissue, enveloping masses of multiplicative forms, spores, pus and cellular debris.

While some of the heavily infected fish have been quite active, others were sluggish and clumsy in their movements. The "sore mouth" condition is obviously a source of pain to the fish, as well as impairing its feeding activities. Similar malnutrition has also been seen in infections of the mouth. Secondary troubles due to compression of the gut, ovary and air bladder by myxosporidian tumours have been observed.

Some skin and subcutaneous tumours due to Myxosporidia rupture to the surface or exterior of the body, causing ulcerations. Such surface ulcers may become the seat of secondary invasion by bacteria and also by fungal growths.

ECONOMIC IMPORTANCE

The economic importance of the occurrence of Myxosporidia in the fresh-water fishes of Quebec may be considered. In many cases young hosts have been affected. Mortality among fry may be more extensive than we have been able to observe and may, perhaps, account for the absence of fish or their great scarcity, in what would appear to be quite suitable waters. Both fry and young adults of the non-game fishes serve as food for frogs, birds, certain other carnivorous fish and fish-eating fur mammals. Restriction of the numbers of these non-game fish may thus ultimately have an effect on the character of the fauna of the neighbourhood.

Some of the Myxosporidia-infected fish serve as food for man. Salmon, trout, perch, pike, pickerel and suckers can be bought in shops in Montreal. The suckers and perch are well distributed in fishing areas. While nothing approaching epizootic form due to Myxosporidia has come under our observation, Myxosporidia as factors of mortality must not be overlooked. The present record of single instances of infection of *Zschokkella*, *Myxobolus* and *Henneguya* from the speckled trout, *Salvelinus fontinalis*, are the first notifications of such infections in this excellent and very palatable game fish. It is suggested that a sharp look-out for myxosporidian infections should be kept in hatcheries, where conditions of crowding and propinquity allow of rapid spread of any disease, which may quickly assume epizootic proportions.

The possibility of spread of Myxosporidia from the non-game fish to game fish also has to be considered. Already *Henneguya fontinalis* has been found in the speckled trout, *Salvelinus fontinalis*, and in the common shiners, *Notropis cornutus* and *N. heterolepis*. Whether the parasite evolved spontaneously in three different hosts in three different localities, or whether mutual cross-infection has occurred, is unknown. The possibilities of such transferences have to be borne in mind.

SUMMARY

The Province of Quebec provides a magnificent field for fresh-water faunistic and ecological research on account of its numerous rivers and lakes. Investigations in ecology and ecological parasitology by the authors have revealed a rich fauna in the areas described herein.

Examinations of fourteen species of fresh-water fish have produced twenty-eight species of Myxosporidia, of which twenty-five are new and three have been already described. The existence of races or strains or varieties of some of the forms is demonstrated.

Descriptions and illustrations are given of twenty-eight Myxosporidia found by the authors in fresh-water fishes of Quebec Province. The new species include: *Sphaerospora notropis*, *Myxidium percae*, *Zschokkella salvelini*, *Myxosoma notropis*, *M. commersonii*, *M. orbitalis*, *M. pfrille*, *M. media*, *M. ellipticoides*, *M. parellipticoides*, *Myxobolus poecilichthidis*, *M. dentium*,

M. percae, *M. rhinichthidis*, *M. notropis*, *M. catostomi*, *M. couesii*, *M. hyborhynchi*, *M. subcircularis*, *M. transversalis*, *M. grandis*, *Henneguya fontinalis*, *H. fontinalis* var. *notropis*, *H. percae*, *H. salmonis* and *H. esocis*. *Myxosoma catostomi* Kudo, *Myxobolus conspicuus* Kudo and *M. ovoidalis* Fantham are described from Canadian fishes. Details are given of a series of races, strains or varieties of *Thelohanellus notatus* Mavor, of *Myxobolus catostomi*, of *M. notropis* and of *Henneguya fontinalis* from other than the original host fish.

The pathology of the myxosporidian infections from the many different situations in the hosts is discussed. Unusual sites of infection are the palatine teeth of *Esox maskinongy* with *Myxobolus dentium* and the iris of the eye of *Couesius plumbeus* with *Myxobolus couesii*.

In connexion with the economic importance of the Myxosporidia found in Quebec fishes, the destruction of young fish, alteration of the character of the fauna dependent on the same, human food supply, possible epizootics in hatcheries and possible cross-infection of game fishes and other fishes of economic importance are considered. The immediate danger is not great; it is the future that may be imperilled.

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EXPLANATION OF PLATES I–X

PLATE I

Untouched photographs of Quebec fishes infected with Myxosporidia.

Fig. 1. *Notropis cornutus* with cyst due to *Myxosoma media* n.sp. filling the dorsal portion of the abdomen and extending laterally on one or both sides of the gut.

Fig. 2. Young *Notropis cornutus* with large cysts of *Myxobolus grandis* n.sp. filling the posterior part of the abdomen and displacing the viscera.

Fig. 3. *Notropis cornutus* with large cyst of *Myxosoma notropis* n.sp. invading the liver and extending into and distending the anterior part of the abdomen.

Fig. 4. *Notropis cornutus* with five cysts, four of *Thelohanellus notatus* Mavor and one of *Sphaerospora notropis* n.sp. Prominent cyst at base of peduncle.

Fig. 5. Young *Notropis cornutus* with large cyst of *Myxosoma orbitalis* n.sp. on the cheek below the eye and extending deep into the orbit, forcing the eye out dorsolaterally and carrying out the suborbital ring.

Fig. 6. *Notropis heterolepis* with subepidermal cysts of *Myxobolus notropis* n.sp. scattered irregularly over the body.

Fig. 7. *Couesius plumbeus* with cyst of *Myxobolus couesii* n.sp. on the iris at the posterodorsal corner of the anterior chamber of the eye.

PLATE II

All figures on Plates II–X were drawn using an Abbé-Zeiss camera lucida. The magnification is 1100 throughout.

Figs. 1–10. *Myxidium percae* n.sp. from *Perca flavescens*. Methyl green stain.

Fig. 1. Pansporoblast with one sporoblast and two spores differentiating.
Fig. 2. Sporoblast with two spores.
Figs. 3–10. Spores of *Myxidium percae* showing differentiation of structure.
Fig. 3. Spore with two sporoplasmic nuclei and one capsulogenous nucleus.
Fig. 4. Wider spore with two linear parietal nuclei.
Fig. 5. Spore showing differentiation of one polar filament and marked longitudinal striae.
Fig. 6. Narrow spore.
Fig. 7. Spore with two coiled polar filaments visible.
Fig. 8. Spore showing suture.
Fig. 9. Group of two large spores.
Fig. 10. Dehiscing spore.

Figs. 11–19. *Zschokkella salvelini* n.sp., from *Salvelinus fontinalis*. Giemsa stain.

Fig. 11. Amoebula.
Fig. 12. Young binucleate pansporoblast.
Figs. 13, 14. Sporoblasts showing nuclear differentiation and beginnings of polar capsules.
Figs. 15, 17. Spores fully formed. Two sporoplasmic and two parietal nuclei shown in Fig. 15. Polar filament coiled in figures of eight.
Fig. 16. Small spore seen at an angle.
Fig. 18. Spore showing suture and full number of nuclei.
Fig. 19. Spore with partly extruded polar filament.

Figs. 20–36. *Myxosoma notropis* n.sp. from *Notropis cornutus*. Figs. 20, 23, 24, 28, 29 stained iron haematoxylin, the rest Giemsa.

Fig. 20. Section of a small portion of liver of *Notropis cornutus* showing many stages of *Myxosoma notropis* in the degenerated liver substance, of which scattered nuclei are present.
Figs. 20–22. Amoebulae with small lobopodia.
Fig. 23. Binucleate pansporoblast.
Fig. 24. Tetranucleate form.
Fig. 25. Multinucleate sporoblast.
Figs. 26, 27. Sporoblasts showing differentiation of two spores.
Figs. 28–36. Spores of *Myxosoma notropis*.
Fig. 28. Spore with two sporoplasmic, two condensed capsulogenous and one parietal nucleus.
Fig. 29. Spore with three parietal nuclei.
Figs. 30, 33, 34. Spores showing fine processes or pseudopodia to the sporoplasm.
Figs. 31, 32, 36. Spores with full complement of nuclei.
Figs. 33–35. Spores with coiled polar filaments.

PLATE III

Figs. 1–7. *Myxosoma commersonii* n.sp. from *Catostomus commersonii*. Giemsa stain.

Figs. 1–4. Stages in development of pansporoblasts and sporoblasts, showing nuclear structure.
Figs. 5, 6. Almost developed spores, the final orientation of structures not yet complete.
Fig. 7. Spore of *Myxobolus commersonii* with sporoplasmic nuclei, minute capsulogenous nuclei and polar filament.

Figs. 8–22. *Myxosoma orbitalis* n.sp. from *Notropis cornutus*. Giemsa stain.

Figs. 8, 10. Uninucleate pansporoblasts.
Fig. 9. Binucleate form.
Fig. 11. Tetranucleate pansporoblast.

Fig. 12. Pansporoblast with sporoblasts.
Fig. 13. Sporoblasts with seven nuclei.
Fig. 14. Older sporoblast with polar capsules and with sporoplasm segregated.
Figs. 15–22. Spores of *Myxosoma orbitalis*.
Fig. 15. Spore with well-marked sporoplasmic nuclei and compact, capsulogenous nuclei.
Figs. 16, 18. Spores with sporoplasmic nuclei arranged tandem.
Figs. 17, 19. Spores showing parietal nuclei.
Figs. 20, 21. Spores with parietal nuclei and polar filaments differentiating.
Fig. 22. Spore with partly extruded polar filament.

Figs. 23–37. *Myxosoma pfrille* n.sp., from *Pfrille neogaeus*. Giemsa stain except Figs. 23, 30, 31, which are stained with iron haematoxylin.

Fig. 23. Small portion of section of cyst showing zonation of stages of *Myxosoma pfrille*.
Fig. 24. Young, uninucleate pansporoblast.
Figs. 25, 26. Uninucleate and binucleate forms.
Figs. 27–29. Pansporoblasts with two sporoblasts differentiating.
Figs. 30, 31. Multinucleate pansporoblasts.
Figs. 32–37. Spores of *Myxosoma pfrille*.
Figs. 32, 33. Two spores showing folded margins. Fig. 33 has but one large sporoplasmic nucleus.
Fig. 34. Spore with one karyosomatic and one compact capsulogenous nucleus.
Fig. 35. Spore with sporoplasmic, capsulogenous and parietal nuclei and some coils of polar filaments.
Fig. 36. Spore with polar filament partly extruded.
Fig. 37. Spore showing sutural ridge and partly extruded polar filament.

Figs. 38–51. *Myxosoma media* n.sp., from *Notropis cornutus*. Figs. 42, 43, 50, 51. Giemsa stain, the remainder iron haematoxylin.

Figs. 38, 39. Uninucleate pansporoblasts.
Fig. 40. Binucleate form.
Figs. 41, 42. Multinucleate form.
Fig. 43. Pansporoblast with two sporoblasts differentiating.
Figs. 44–51. Spores of *Myxosoma media*.
Fig. 46. Spore with elongate, rod-like parietal nuclei.
Figs. 47, 49. Spores with large polar capsules.
Figs. 48, 51. Spores with coiled polar filaments.
Fig. 50. Spore with one large parietal nucleus.
Fig. 51. Spore with pseudopodial sporoplasm.

Figs. 52–60. *Myxosoma ellipticoides* n.sp. from *Catostomus commersonii*. Giemsa stain.

Fig. 52. Binucleate pansporoblast.
Fig. 53. Sporoblast.
Figs. 54–60. Spores of *Myxosoma ellipticoides*. All show large parietal nuclei.
Figs. 54, 58. Spores with subequal polar capsules.
Figs. 55, 56. Spores with transversely parallel sporoplasmic nuclei.
Fig. 57. Spore with one karyosomatic and one compact capsulogenous nucleus.
Fig. 59. Spore with sporoplasmic nuclei arranged tandem.
Fig. 60. Spore with one empty polar capsule and one showing some coils of the polar filament.

PLATE IV

Figs. 1–6. *Myxosoma parellipticoides* n.sp. from *Pfrille neogaeus*. Giemsa stain.

Figs. 1–5. Spores with small sporoplasmic nuclei.
Figs. 1–3. Spores with compact capsulogenous nuclei.
Fig. 5. Spore with two well-marked parietal nuclei.
Fig. 6. Large spore.

Figs. 7–21. *Myxosoma catostomi* Kudo from *Catostomus commersonii*. Iron haematoxylin stain.

Fig. 7. Portion of section of infected muscle of *Catostomus commersonii* showing zonation and various stages of *Myxosoma catostomi*.

Fig. 8. Young uninucleate pansporoblast.

Fig. 9. Young pansporoblast with dividing nucleus.

Figs. 10–12. Binucleate forms.

Figs. 13, 14. Further stages in nuclear division.

Figs. 15–21. Spores.

Figs. 15, 21. Spores with rounded capsulogenous nuclei.

Fig. 16. Spore enclosed in remains of sporoblast.

Figs. 16–18. Spores with parietal nuclei.

Figs. 17, 18, 20. Spores showing foldings or thickenings of sporocyst.

Figs. 22–43. *Sphaerospora notropis* n.sp. from *Notropis cornutus* and *Catostomus commersonii*. Giemsa stain.

Fig. 22. Uninucleate pansporoblast.

Figs. 23–26. Pansporoblasts differentiating into two sporoblasts.

Figs. 27–29. Sporoblasts.

Figs. 30–43. Spores.

Fig. 30. Spore with dense sporoplasm and distinct sporoplasmic nuclei.

Fig. 31. Spore with one parietal nucleus.

Figs. 32, 33. Spores with two parietal nuclei.

Fig. 34. Spore with full number of nuclei.

Figs. 37, 38, 40. Spores showing coils of polar filaments and one or both capsulogenous nuclei.

Figs. 39, 41. Spores with slightly unequal polar capsules.

Fig. 42. Spore showing sutural ridge.

Fig. 43. Spore with one polar filament partly discharged.

PLATE V

Figs. 1–14. *Myxobolus poecilichthidis* n.sp. from *Poecilichthys exilis*. Figs. 1, 8, 9. Giemsa stain; Figs. 10–13, Delafield haematoxylin, the rest methylene blue.

Fig. 1. Amoebula.

Figs. 2–14. Spores.

Fig. 2. Spore with sporoplasmic nuclei arranged tandem, two compact parietal and two compact capsulogenous nuclei.

Fig. 3. Spore with sporoplasmic nuclei arranged transversely parallel.

Figs. 6, 11, 13. Spores showing coiled polar filaments and sutural ridge.

Figs. 7, 9. Spores showing polar filaments.

Fig. 8. Spore with karyosomatic capsulogenous nuclei.

Fig. 14. Spore with one collapsed polar capsule and most of the polar filament extruded.

Figs. 15–32. *Myxobolus dentium* n.sp. from *Esox maskinongy*. Giemsa stain.

Figs. 15, 16. Amoebulae.

Fig. 17. Binucleate pansporoblast.

Figs. 18, 19. Multinucleate pansporoblasts.

Fig. 20. Pansporoblast with cytoplasm and nuclei segregating to form two sporoblasts.

Figs. 21, 22. Spores differentiating within sporoblasts. Seen in section.

Fig. 23. Two spores within sporoblast.

Figs. 24–32. Spores of *Myxobolus dentium*.

Fig. 24. Spore with compact capsulogenous nuclei far down on the polar capsules and two compact parietal nuclei.

Fig. 25. Spore with karyosomatic capsulogenous nuclei.

Fig. 26. Spore with one large parietal or valvular nucleus.

Fig. 27. Spore with small portions of both polar filaments extruded.

Fig. 28. Spore showing sutural ridge.
Figs. 29, 31. Spores with coiled polar filaments.
Fig. 32. Two spores with polar filaments extruded and tangled together.

Figs. 33–47. *Myxobolus percae* n.sp. from *Perca flavescens*. Giemsa stain.

Figs. 33, 34. Multinucleate pansporoblasts.
Fig. 35. Pansporoblast with two spores.
Figs. 36–47. Spores.
Figs. 36, 37. Small spores.
Fig. 38. Spore with one polar filament partly extruded.
Figs. 39, 40. Spores with distinct karyosomatic capsulogenous nuclei.
Figs. 42, 44. Spores with parietal nuclei.
Fig. 45. Spore with coiled polar filament.
Fig. 47. Spore showing sutural ridge.

Figs. 48–61. *Myxobolus rhinichthidis* n.sp. from *Rhinichthys atronasus*.

Fig. 48. Very small portion of cyst showing zonation of stages of *Myxobolus rhinichthidis*. Iron haematoxylin stain.
Fig. 49. Uninucleate pansporoblast.
Fig. 50. Binucleate pansporoblast.
Figs. 51, 52. Tetranucleate forms.
Fig. 53. Sporoblast with two spores differentiating.
Figs. 54–61. Spores.
Figs. 54, 56. Spores with karyosomatic capsulogenous nuclei.
Figs. 58, 60. Spores with thickenings on edge. Unusual.
Fig. 59. Spore with coiled polar filament.
Fig. 61. Spore showing sutural ridge.

PLATE VI

Figs. 1–12. *Myxobolus notropis* n.sp. from *Notropis heterolepis*. Iron haematoxylin.

Fig. 1. Portion of section of cyst showing trophozoites.
Fig. 2. Tetranucleate pansporoblast.
Fig. 3. Multinucleate form.
Figs. 4, 5. Pansporoblasts with two sporoblasts differentiating into spores.
Figs. 6–12. Spores of *Myxobolus notropis*.
Fig. 6. Spore with two sporoplasmic, two karyosomatic capsulogenous and two compact parietal nuclei.
Figs. 7–9. Spores showing prolongations of sporoplasm.
Fig. 10. Spore with tandem sporoplasmic nuclei and parts of polar filaments showing.
Fig 11. Spore with marked sporoplasmic processes and three compact parietal nuclei.
Fig. 12. Spore in section showing sutural ridge.

Figs. 13–34. *Myxobolus catostomi* n.sp. from *Catostomus commersonii*.

Fig. 13. Portion of section of subepithelial cyst above the basihyal bone of Catostomus, showing zonation of various stages of the parasite.
Fig. 14. Amoebula.
Fig. 15. Uninucleate pansporoblasts.
Figs. 16, 17. Binucleate pansporoblasts.
Figs. 18–22. Multinucleate pansporoblasts showing various stages of nuclear differentiation.
Fig. 23. Pansporoblast with two sporoblasts differentiating.
Fig. 24. Sporoblast with polar capsules beginning to form.
Figs. 26–34. Spores of *Myxobolus catostomi*.
Fig. 26. Spore showing tandem sporoblastic nuclei and capsulogenous nuclei.
Figs. 27, 30. Spores with one coiled polar filament showing.

Fig. 29. Spore in section showing sutural ridge.
Figs. 31, 32. Spores with subequal polar capsules.
Fig. 33. Spore with two parietal nuclei.
Fig. 34. Spore showing two sporoplasmic nuclei, one parietal nucleus, two compact capsulogenous nuclei and coils of both polar filaments.

Figs. 35–41. *Myxobolus couesii* n.sp. from *Couesius plumbeus*. Iron haematoxylin stain.

Fig. 35. Portion of section of cyst showing large nuclei of the iris and zonation of young pansporoblasts.
Figs. 36, 37. Multinucleate pansporoblasts.
Fig. 39. Pansporoblast with two spores.
Figs. 40, 41. Spores of *Myxobolus couesii*.

Figs. 42–48. *Myxobolus notropis* from *Notropis cornutus*. Giemsa stain.

Fig. 42. Spore with full complement of nuclei.
Figs. 43, 44. Spores with smaller and larger sporoplasmic nuclei.
Figs. 44, 47. Spores showing processes of sporoplasm.
Figs. 47, 48. Spores with small and larger iodinophilous vacuoles.

Figs. 49–55. *Myxobolus hyborhynchi* n.sp. from *Hyborhynchus notatus*. Giemsa stain.

Figs. 49, 51–55. Show various appearances of polar filaments in the long polar capsules.
Figs. 49, 50, 55. Spores showing valvular nuclei.
Figs. 52, 53. Spores showing capsulogenous nuclei.
Fig. 55. Spore with one polar filament beginning to extrude.

Figs. 56–62. *Myxobolus catostomi* from *Catostomus commersonii*. Giemsa stain.

Fig. 56. Binucleate pansporoblast.
Figs. 57–62. Spores of *Myxobolus catostomi*.
Figs. 57, 60, 61. Spores showing valvular nuclei.
Figs. 57, 62. Spores showing polar filaments.
Fig. 60. Spore showing sporoplasmic prolongations.
Figs. 61, 62. Spores with capsulogenous nuclei.

PLATE VII

Figs. 1–14. *Myxobolus subcircularis* n.sp. from *Catostomus commersonii*. Giemsa stain.

Fig. 1. Amoebula.
Figs. 2, 3. Binucleate forms.
Fig. 4. Binucleate form with potential karyosomes of other nuclei. Binucleate form with nuclei in different phases of division.
Figs. 6–14. Spores of *Myxobolus subcircularis*.
Fig. 6. Spore with two sporoplasmic nuclei, two rounded parietal nuclei and two capsulogenous nuclei.
Figs. 7, 11, 12. Spores with one large parietal nucleus.
Figs. 8, 9, 11. Spores with portions of polar filaments stained.
Fig. 10. Spore with unequal polar capsules.
Fig. 12. Spore with rounded, karyosomatic capsulogenous nuclei.
Fig. 14. Spore with most of its polar filaments extruded.

Figs. 15–21. *Myxobolus transversalis* n.sp. from *Notropis cornutus*. Giemsa stain.

Fig. 15. Spore showing sporoplasmic nuclei and small vacuole.
Figs. 16, 17. Spores with compact capsulogenous nuclei.
Fig. 17. Spore with two oval parietal nuclei.
Figs. 18, 20. Spores with polar filaments differentiating.

Figs. 22–37. *Myxobolus conspicuus* Kudo from *Moxostoma aureolum*. Giemsa stain.

Fig. 22. Group of three pansporoblasts.
Figs. 23, 24. Binucleate pansporoblasts.
Figs. 25, 26. Multinucleate pansporoblasts.
Figs. 27–37. Spores.
Figs. 27–32. Spores with well-marked folds or thickenings of margin.
Figs. 27, 32, 33. Spores with sporoplasmic nuclei arranged tandem.
Figs. 28, 37. Spores with sporoplasmic nuclei arranged transversely.
Figs. 28, 31. Spores with polar filaments showing in part.
Figs. 29, 33, 36. Spores with sporoplasmic nuclei arranged obliquely.
Figs. 34, 35. Spores showing sutural ridge.

Figs. 38–53. *Myxobolus grandis* n.sp. from *Notropis cornutus*. Giemsa stain.

Fig. 38. Uninucleate pansporoblast.
Figs. 39, 40. Binucleate pansporoblasts.
Fig. 41. Amoebula with pseudopodia.
Fig. 42. Multinucleate pansporoblast.
Fig. 43. Pansporoblast with two sporoblasts differentiating.
Figs. 44–52. Spores of *Myxobolus grandis*.
Fig. 44. Spore with sporoplasmic nuclei arranged tandem.
Fig. 45. Spore with sporoplasmic nuclei arranged transversely.
Fig. 46. Spore with small, compact parietal and capsulogenous nuclei.
Figs. 47–51. Spores with differentiating polar filaments.
Figs. 48, 51. Spores with one large parietal nucleus.
Fig. 49. Spore with two large parietal nuclei.
Figs. 52, 53. Spores with one polar filament partly extruded.

Figs. 54–65. *Myxobolus ovoidalis* Fantham from *Salvelinus fontinalis*. Fresh methyl green preparations and iron haematoxylin.

Fig. 54. Binucleate pansporoblast.
Fig. 55. Pansporoblast with two sporoblasts differentiating.
Fig. 56. Pansporoblast with two spores.
Figs. 57–63. Spores of *Myxobolus ovoidalis*. Sporoplasmic nuclei with well-marked chromatin on the nuclear membranes and relatively long polar capsules.
Figs. 58, 59. Spores with one parietal nucleus and coiled polar filament.
Figs. 57, 60–64. Spores with rounded, karyosomatic capsulogenous nuclei.
Figs. 60, 62. Spores with small compact capsulogenous nuclei.
Fig. 65. Spore with one partly extruded polar filament.

PLATE VIII

Figs. 1–18. *Thelohanellus notatus* Mavor from *Notropis cornutus* from the Nicolet River at St Clothilde. Giemsa stain.

Fig. 1. Uninucleate pansporoblast.
Fig. 2. Binucleate pansporoblast.
Fig. 3. Part of section of cyst, showing zonation of parasites.
Figs. 3–7. Multinucleate pansporoblasts.
Figs. 8–10. Pansporoblasts with sporoblasts and spores differentiating.
Fig. 10. Disporous sporoblast.
Figs. 11–18. Spores of *Thelohanellus notatus*.
Figs. 11–13, 15, 16. Spores with coiled polar filaments.
Figs. 11, 13, 14. Spores showing valvular nuclei.
Figs. 12, 15, 17. Spores with tandem sporoplasmic nuclei.
Fig. 14. Spore showing sutural ridge.

Fig. 15. Spore with valves dehiscing.
Fig. 18. Spore with most of its polar filament extruded.

Figs. 19–24. *Thelohanellus notatus* Mavor from *Notropis cornutus* from Rivière des Pins. Giemsa stain.

Fig. 19. Amoebula with lobopodia.
Fig. 20. Multinucleate pansporoblast.
Fig. 21. Multinucleate pansporoblasts with four sporoblasts and spores differentiating.
Figs. 22–24. Spores showing variations in the positions of the nuclei.
Fig. 24. Spore with second capsulogenous nucleus.

Figs. 25–31. *Thelohanellus notatus* Mavor from *Notropis cornutus* from Nicolet River. Giemsa stain.

Fig. 25. Pansporoblast forming two sporoblasts.
Fig. 26. Sporoblast with two spores.
Figs. 27–31. Spores of *Thelohanellus notatus*.
Figs. 27, 29, 31. Spores with sporoplasmic nuclei tandem.
Fig. 28. Spore with sporoplasmic nuclei transverse.
Fig. 30. Spore with apparently only one sporoplasmic nucleus and with sporoplasmic processes.
Fig. 31. Spore with small part of polar filament extruded.

Figs. 32–38. *Thelohanellus notatus* Mavor from *Pfrille neogaeus* from the Ulverton River.

Figs. 32, 38. Spores with transverse sporoplasmic nuclei.
Figs. 33–37. Spores with tandem sporoplasmic nuclei.
Figs. 33, 37. Spores with karyosomatic capsulogenous nuclei.

Figs. 39–53. *Thelohanellus notatus* Mavor from *Notropis cornutus* from Rivière des Rosières. Figs. 45, 50–53. Giemsa stain; Figs. 39–44, 46–49. Iron haematoxylin stain.

Fig. 39. Small portion of cyst showing pansporoblasts.
Figs. 40, 41. Young pansporoblasts.
Figs. 42–44. Multinucleate pansporoblasts.
Figs. 45, 46. Sporoblasts containing two spores.
Figs. 47, 49, 53. Spores with two sporoplasmic, two parietal and two capsulogenous nuclei.
Figs. 48–53. Spores.
Figs. 48–50, 53. Spores with tandem sporoplasmic nuclei.
Figs. 48, 50, 52, 53. Spores showing portions of coiled polar filaments.
Fig. 51. Spore showing sutural ridge.
Fig. 52. Spore with transverse sporoplasmic nuclei.

Figs. 54–66. *Thelohanellus notatus* Mavor from *Hyborhynchus notatus* from Rivière des Pins. Iron haematoxylin stain.

Fig. 54. Amoebula with long pseudopodia.
Fig. 55. Young pansporoblast.
Figs. 56, 57. Multinucleate pansporoblasts.
Fig. 58. Pansporoblast with two sporoblasts differentiating.
Figs. 59–66. Spores.
Figs. 61–64. Spores with two parietal or valvular nuclei.
Fig. 63. Spore with two potential capsulogenous nuclei.
Figs. 65, 66. Spores with karyosomatic capsulogenous nuclei.
Fig. 66. Spore with one parietal nucleus.

Fig. 67. *Thelohanellus notatus* Mavor from *Notropis cornutus* from Alder Brook. One small spore of Thelohanellus in which two polar capsules have formed. Iron haematoxylin stain.

PLATE IX

Figs. 1–8. *Henneguya fontinalis* n.sp. from *Salvelinus fontinalis*.

Fig. 1. Amoebula.
Fig. 2. Pansporoblast containing two spores.
Figs. 3–8. Spores of *Henneguya fontinalis*.
Fig. 3. Spore with one karyosomatic and one compact capsulogenous nucleus.
Figs. 4, 6, 8. Spores showing parietal nuclei near the caudal appendage.
Fig. 4. Spore showing some coils of polar filament.
Fig. 5. Spore with sporoplasmic nuclei almost tandem.
Fig. 6. Spore with full complement of nuclei.
Fig. 7. Spore with large capsulogenous nuclei.
Fig. 8. Spore with parts of both polar filaments extruded.

Figs. 9–21. *Henneguya fontinalis* var. *notropis* from *Notropis cornutus*. Giemsa stain.

Fig. 9. Pansporoblast with two sporoblasts differentiating.
Fig. 10. Pansporoblast with two spores.
Figs. 11–21. Spores of *Henneguya fontinalis* var. *notropis*.
Fig. 11. Spore with all nuclei visible.
Fig. 12. Spore with subequal sporoplasmic nuclei, capsulogenous nuclei, two parietal nuclei at the base of the caudal process and an additional parietal nucleus in the caudal process.
Figs. 13, 15. Spores with karyosomatic and capsulogenous nuclei.
Figs. 16, 17. Spores with large capsulogenous nuclei.
Fig. 18. Spore with small, compact capsulogenous nuclei.
Fig. 19. Spore with one parietal nucleus.
Fig. 20. Spore showing part of polar filament.
Fig. 21. Broad spore.

Fig. 22. Spore of *Henneguya fontinalis* var. *notropis* from *Notropis heterolepis*. Iron haematoxylin stain.

Figs. 23–37. *Henneguya percae* n.sp. from *Perca flavescens*. Methyl green stain.

Fig. 23. Amoebula with pseudopodia.
Fig. 24. Young pansporoblasts with two nuclei in process of further division.
Fig. 25. Tetranucleate pansporoblast.
Fig. 26. Pansporoblast forming two sporoblasts.
Fig. 27. Pansporoblast with two spores.
Figs. 28–37. Spores of *Henneguya percae*.
Figs. 28, 30. Spores with transverse karyosomatic sporoplasmic nuclei and karyosomatic capsulogenous nuclei.
Fig. 29. Spore with compact capsulogenous nuclei and tandem sporoplasmic nuclei.
Fig. 30. Almost pentagonal spore.
Fig. 31. Spore showing part of polar filament.
Fig. 32. Spore with narrow polar capsules.
Fig. 33. Spore with wide polar capsules.
Fig. 34. Almost hexagonal spore.
Figs. 35, 36. Spores with coiled polar filaments.
Fig. 37. Spore with partly extruded polar filament.

PLATE X

Figs. 1–6. *Henneguya salmonis* n.sp. from *Salmo salar*. Methyl green stain.

Fig. 1. Spore with caudal appendages apposed.
Fig. 2. Spore with full complement of nuclei.
Fig. 3. Spore with karyosomatic capsulogenous nuclei.

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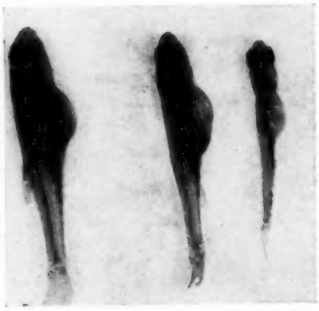

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Fish with Myxosporidian infections.

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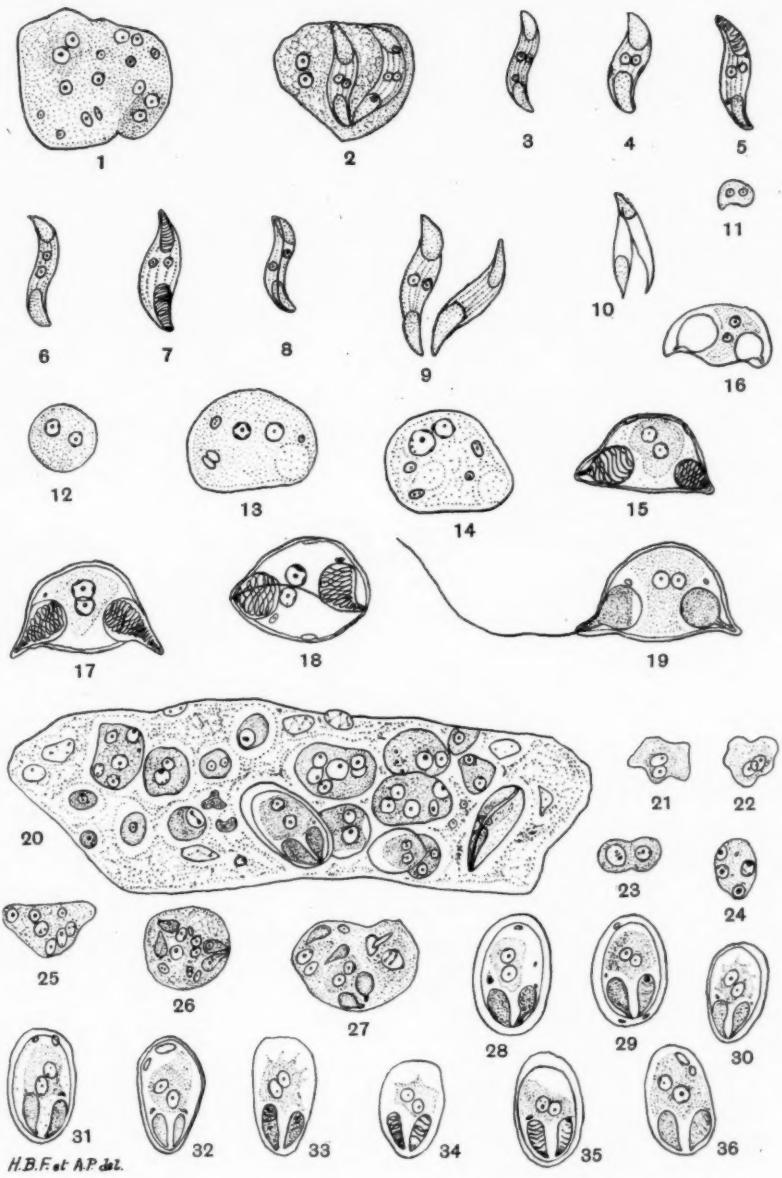

Figs. 1–10. *Myxidium percae* n.sp. Figs. 11–19. *Zschokkella salvelini* n.sp.
Figs. 20–36. *Myxosoma notropis* n.sp.

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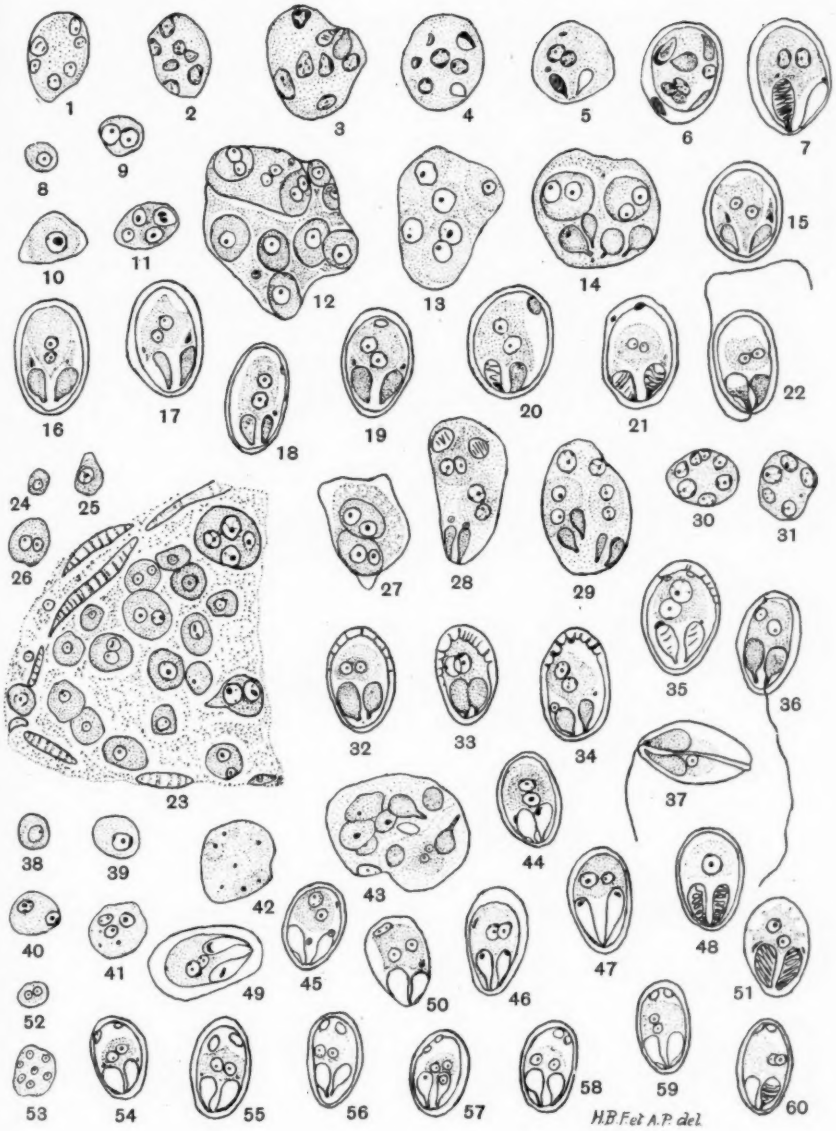

Figs. 1–7. *Myxosoma commersonii* n.sp. Figs. 8–22. *M. orbitalis* n.sp.
Figs. 23–37. *M. pfrille* n.sp. Figs. 38–51. *M. media* n.sp.
Figs. 52–60. *M. ellipticoides* n.sp.

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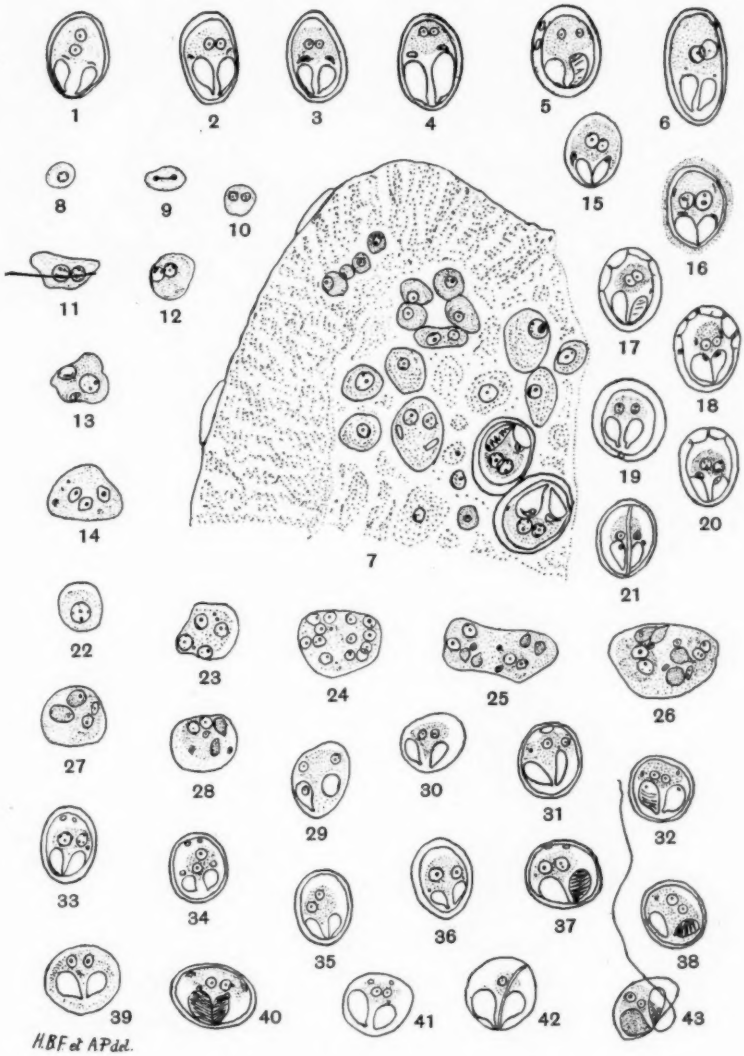

Figs. 1–6. *Myxosoma parellipticoides* n.sp. Figs. 7–21. *M. catostomi* Kudo.
Figs. 22–43. *Sphaerospora notropis* n.sp.

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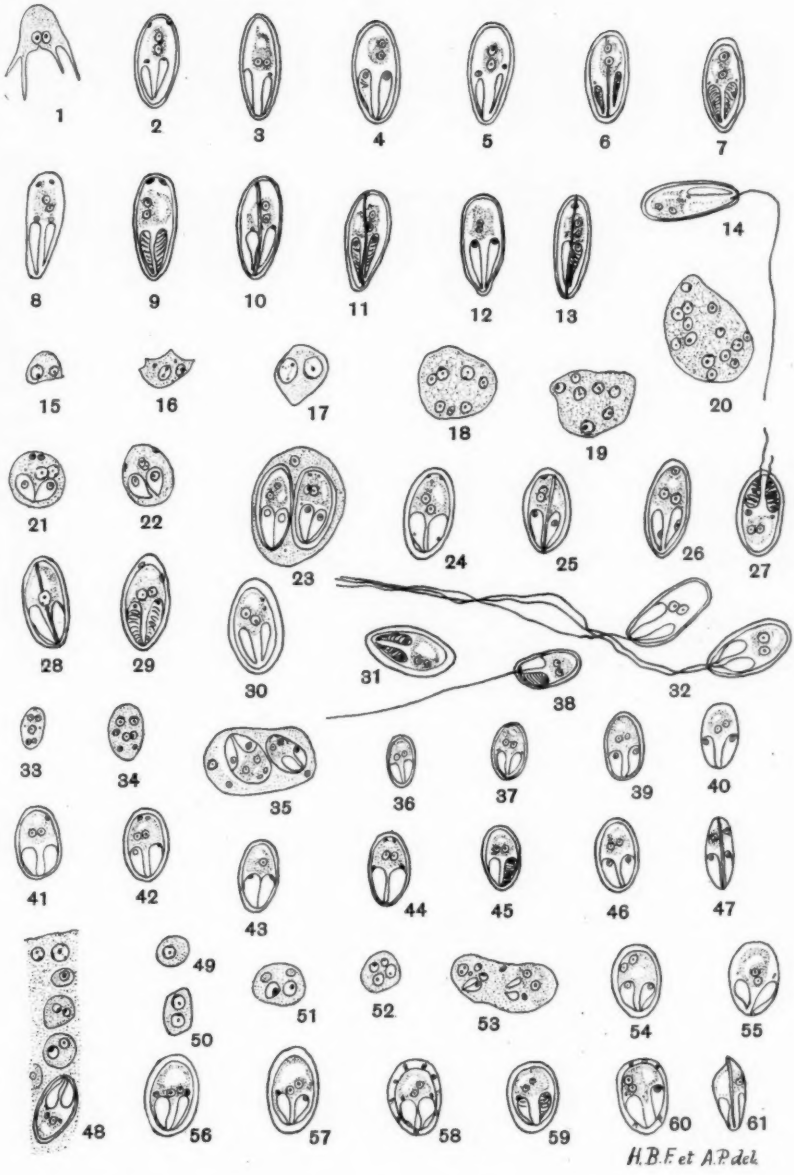

Figs. 1–14. *Myxobolus poecilichthidis* n.sp. Figs. 15–32. *M. dentium* n.sp.
Figs. 33–47. *M. percae* n.sp. Figs. 48–61. *M. rhinichthidis* n.sp.

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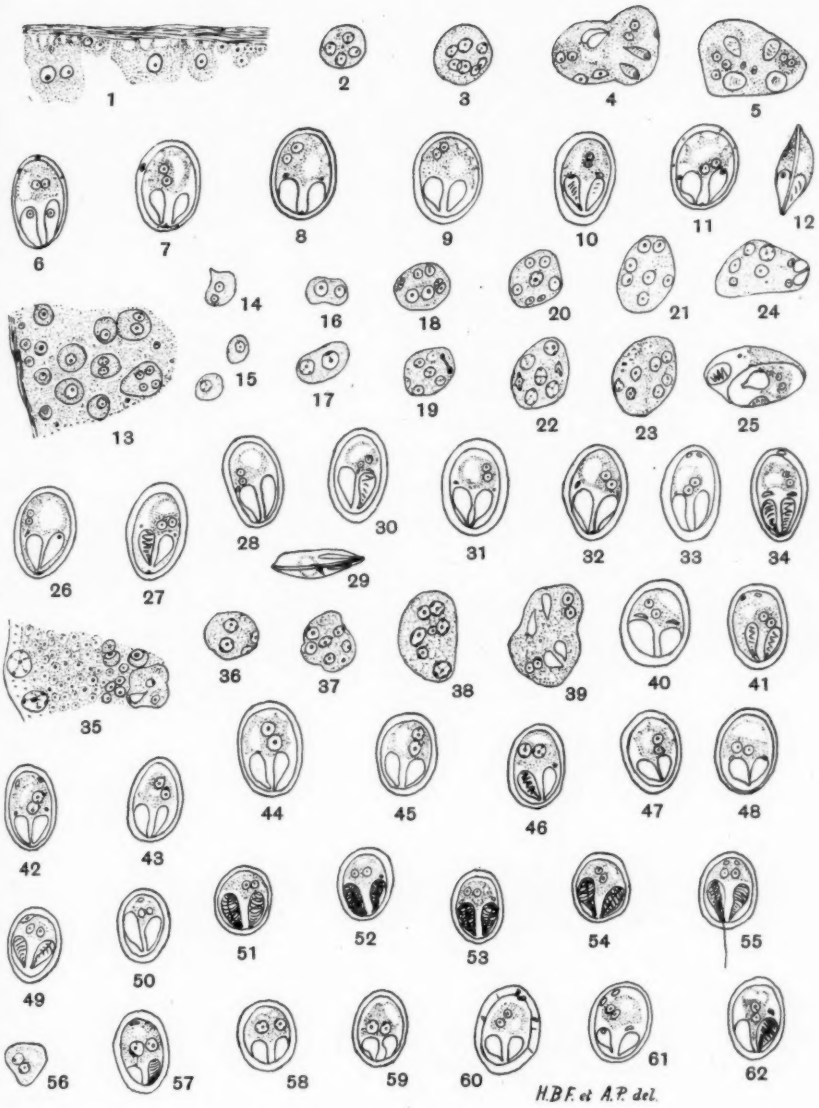

Figs. 1–12. *Myxobolus notropis* n.sp.
Figs. 13–34. *M. catostomi* n.sp.
Figs. 35–41. *M. couesii* n.sp.
Figs. 42–48. *M. notropis* n.sp.
Figs. 49–55. *M. hyborhynchi* n.sp.
Figs. 56–62. *M. catostomi* var.

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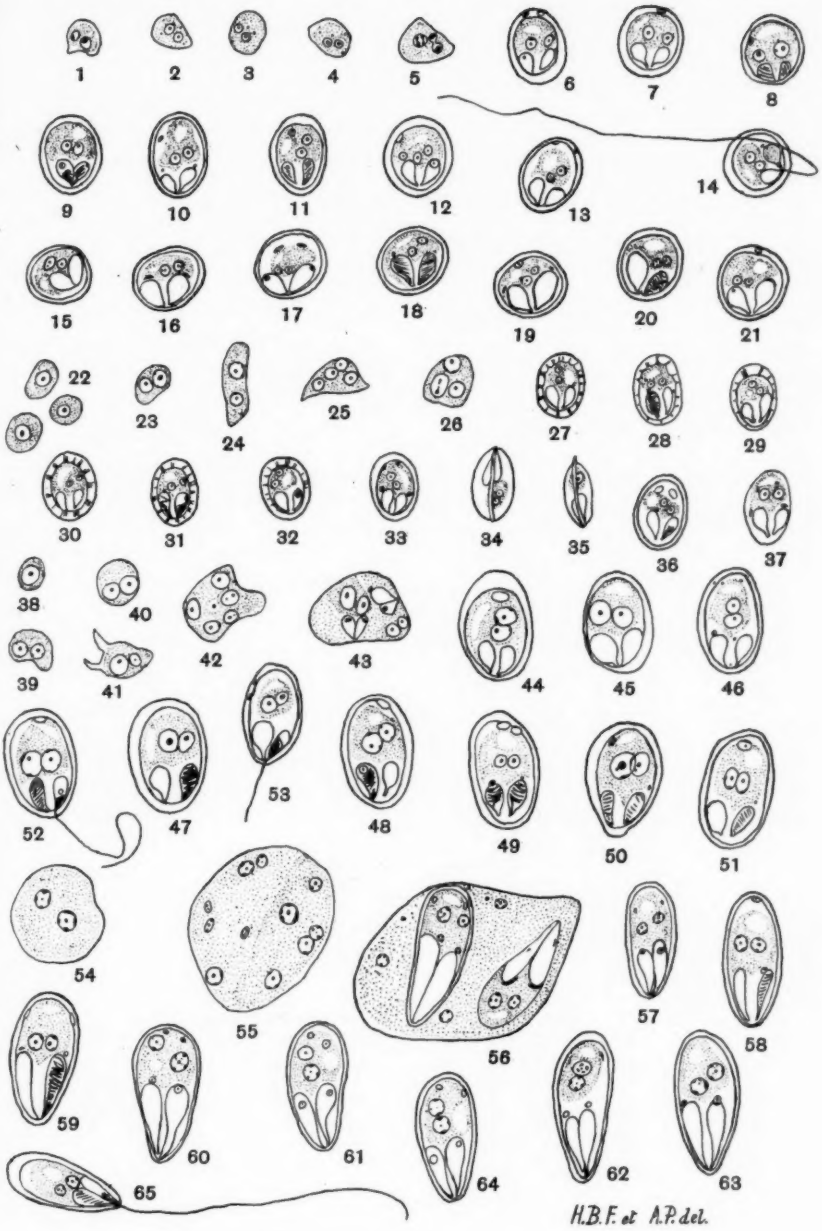

Figs. 1–14. *Myxobolus subcircularis* n.sp. Figs. 15–21. *M. transversalis* n.sp.
Figs. 22–37. *M. conspicuus* Kudo. Figs. 38–53. *M. grandis* n.sp.
Figs. 54–65. *M. ovoidalis* Fantham.

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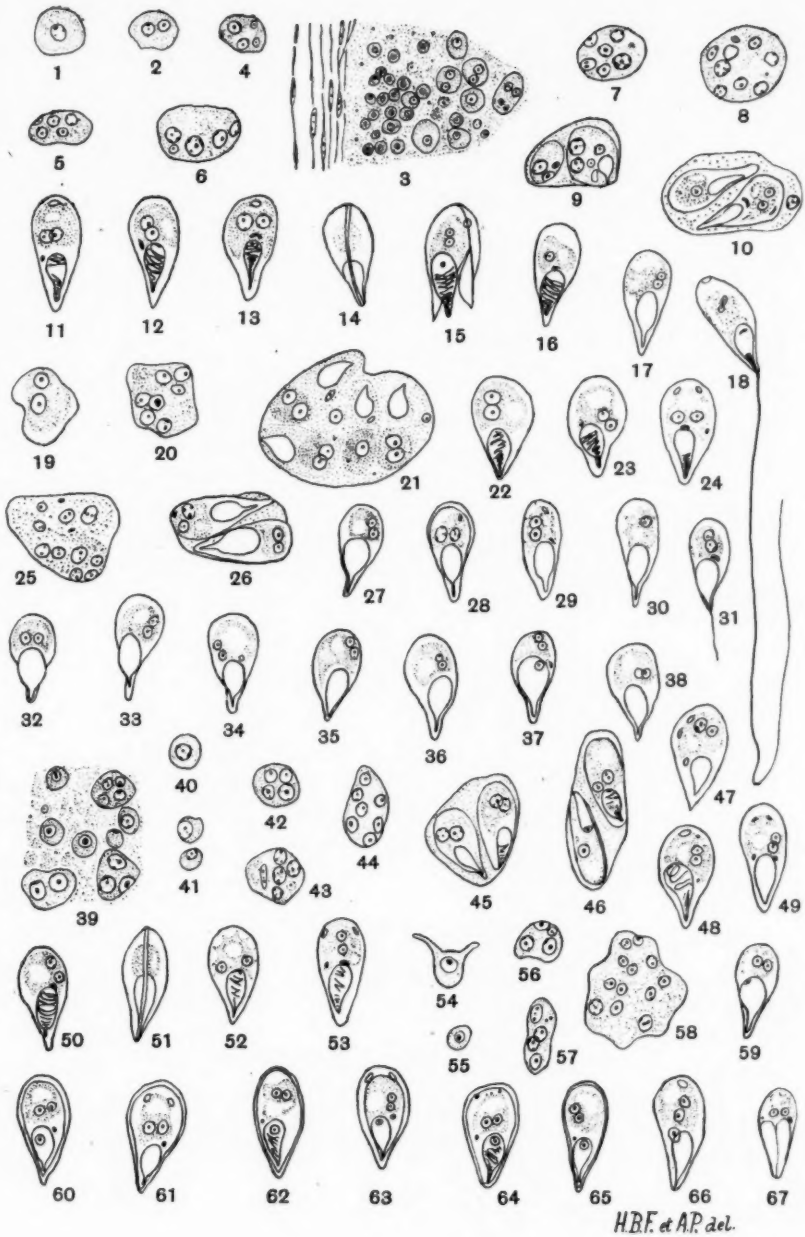

Thelohanellus notatus Mavor.

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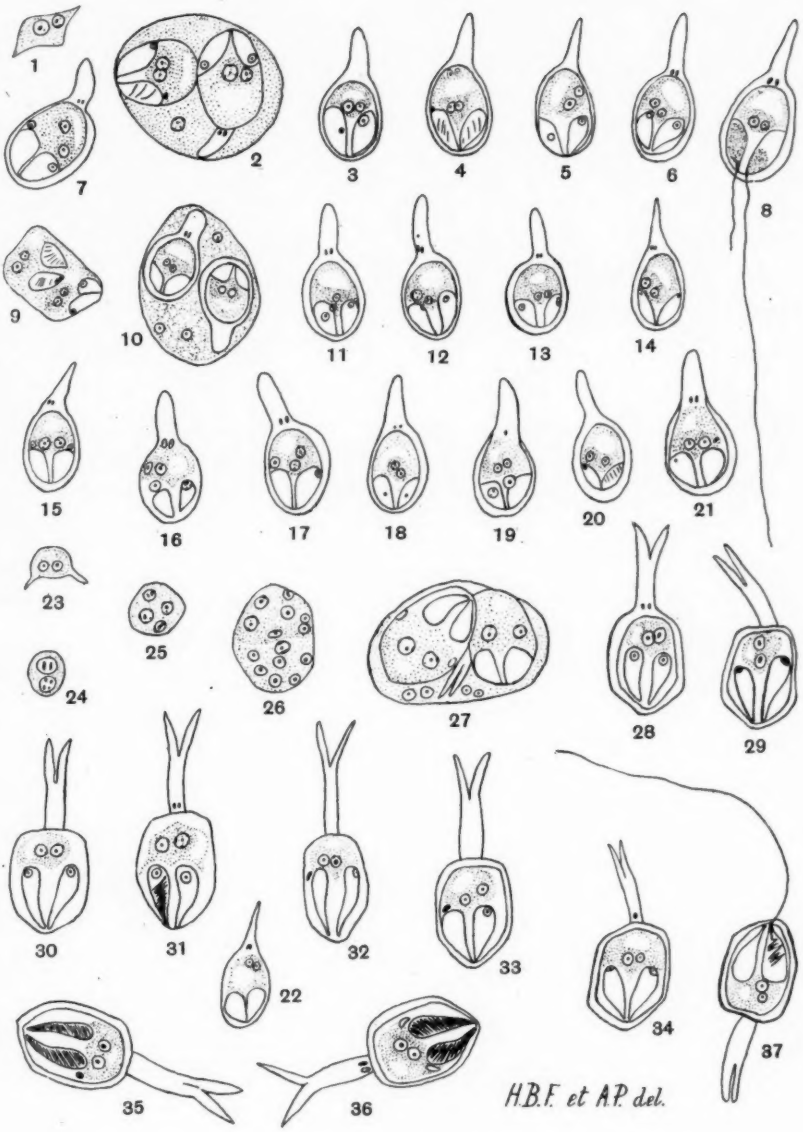

Figs. 1–8. *Henneguya fontinalis* n.sp. Figs. 9–22. *H. fontinalis* var. *notropis*.
Figs. 23–37. *H. percae* n.sp.

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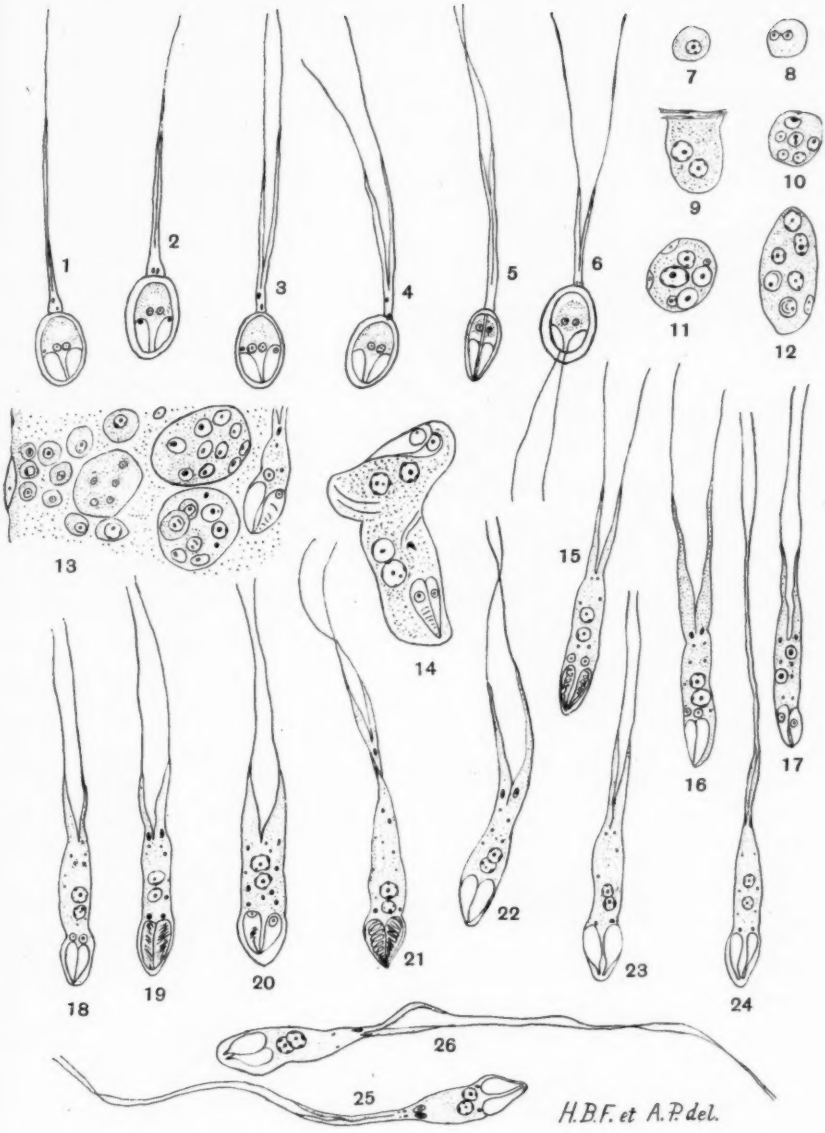

Figs. 1–6. *Henneguya salmonis* n.sp.

Figs. 7–26. *H. esocis* n.sp.

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Fig. 4. Spore with processes separated.
Fig. 5. Spore showing suture.
Fig. 6. Spore with both polar filaments partly extruded.

Figs. 7–26. *Henneguya esocis* n.sp. from *Esox niger*. Figs. 7–13. Ehrlich haematoxylin. Figs. 14–26. Methylene blue stain.

Fig. 7. Uninucleate pansporoblast.
Fig. 8. Binucleate pansporoblast.
Fig. 9. Trophozoite attached to wall.
Figs. 10–12. Multinucleate forms.
Fig. 11. Sporoblast in section.
Fig. 12. Sporoblast with nuclei for two spores differentiating.
Fig. 13. Portion of section of cyst showing zonation of different stages of *Henneguya esocis*.
Fig. 14. Disporous sporoblast forming spores.
Figs. 15–26. Spores of *Henneguya esocis*, all with tandem sporoplasmic nuclei.
Figs. 15–21. Spores with full complement of nuclei, showing variations in morphology.
Figs. 15, 19, 21. Spores with coiled polar filaments.
Fig. 20. Broad spore.
Figs. 21–23. Spores showing flexing of caudal appendages.
Figs. 24–26. Spores with long processes.

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BIOLOGY, MORPHOLOGY AND ANATOMY OF APHIDOPHAGOUS SYRPHID LARVAE

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From the Molteno Institute of Biology and Parasitology, University of Cambridge

(With 75 Figures in the Text)

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Introduction

In spite of the fact that a large amount of interesting work has been done on Syrphidae, the information available in the literature on morphology and anatomy of their larvae is incomplete and fragmentary. In this paper an attempt has been made to describe the most common species of syrphid larvae found in Cambridge, which live on aphids. The species dealt with in this paper are *Syrphus luniger* Meig., *Syrphus balteatus* De Geer, *Syrphus ribesii* Linne, *Catabomba pyrastri* Linne, *Sphaerophoria flavicauda* Zett., *Sphaerophoria scripta* Linne and *Platychirus scutatus* Meig. The external morphology and cephalopharyngeal armature of third stage larvae of all these species have been described, but the early stages of only one species, i.e. *Syrphus luniger* are considered. For the study of anatomy *Platychirus scutatus* was mainly used, since this species was most easily obtained at almost all times of the year. An account of the characteristic features and general habits of each of the species listed above is also given. Great care has been taken in drawing the figures, in order to avoid lengthy descriptions.

The life histories of some species of syrphid larvae have been followed by Metcalf (1913, 1917), but his descriptions and figures of the buccopharyngeal armature are incomplete and inadequate. Krüger (1926) gives lengthy descriptions of their habits, but deals only very briefly with the morphology of some species, and the few figures he gives are unsatisfactory. One gets a clear conception of the mouth-parts and pharyngeal skeleton of a syrphid larva for the first time from Keilin's work on cyclorraphous dipterous larvae (Keilin, 1915). In addition to the discovery of the remarkably close relationship between the form of the cephalopharyngeal skeleton and habits of the larvae, Keilin revealed the presence of a characteristic fibrillar tissue on the surface of the salivary gland of the carnivorous anthomyid and syrphid larvae. I am greatly indebted to him for his kindness in allowing me the use of some of his unpublished records on syrphid larvae.

The only other important work on the anatomy of syrphid larvae is that of Künckel d'Herculais (1875) on the development of Volucellinae.

MATERIAL AND METHODS

The simplest and most important procedure for the study of the morphology of the larvae is to anaesthetize them with chloroform for 5–10 min., or to immerse them in water at 50° C. for about 15 min., then mount them in distilled water on a slide and cover with a cover-slip, the latter being placed in such a way that the posterior end of the larva is covered before the anterior. By this means the larva is extended anteriorly and the anterior segments and pseudocephalon can be easily seen. For the study of chitinous structures the larva was fixed, cut in two and macerated in cold 5% KOH for about 24 hr. At the end of this time the KOH was stirred in the region of the cut end, in order to wash out the remaining undissolved soft tissue. When absolutely clean it was washed in 30% alcohol, taken up to 90% alcohol, then stained in 5% solution of acid fuchsin in 90% alcohol for 2–5 min. If overstained it was returned to 90% alcohol for a few minutes, then completely dehydrated and cleared in xylol or cedarwood oil. In many cases specimens were preserved in cedarwood oil instead of making permanent mounts, as it is then possible to examine them from all angles. An excellent method of fixing a larva with its head and body completely extended is as follows: Wet the living larva thoroughly, pick it up with a wet camel's hair brush and let it crawl towards the handle, immerse it quickly (posterior end first) for a few seconds in hot water. After a couple of minutes transfer it to 90% alcohol. The disadvantage of this method is that the cuticle becomes detached at many points from the underlying soft parts, and the larva tends to become dark when kept in alcohol for long periods.

Carnoy's was found to be the best fixative for studying anatomy and histology; larvae were left for about 15 min. in Carnoy's at 40° C., then washed for about an hour in 90% alcohol. Mann's stain, haemalum and Delafield's haematoxylin were the stains most commonly used.

Biology

In summer most of the larvae described may be found on leaves of cabbages, sprouts, currants, plums, roses, mulberry and thistle, usually in association with aphids. There is a distinct tendency for them to live on the undersurface of the leaves. This position may be due either to the fact that aphids are mostly present on the undersurface, or that the larvae are negatively heliotropic. They are often found lying motionless in a fold or depression on the leaf.

Syrphid larvae are characterized by their colour and markings, which are typical for each species. The colour of the larva in most cases is not due to pigmentation of the skin but to colouring matter which is usually present in the fat-body, especially in that part which lies near the dorsal surface of the larva and shows a characteristic arrangement in each species. In a few cases, in addition to the fat-body, the body fluid and the malpighian tubes also contain colouring matter.

Some of the larvae are able to move remarkably rapidly. As they move they moisten the surface with saliva, which appears to help their progress in some way. If a larva is left on a clean surface the saliva can be seen as a shining streak along the path traversed. A larva travels with a characteristic looping movement, the degree of its activity being influenced by moisture on the leaf.

When in search of food a syrphid larva fixes its anal end to the surface on which it happens to be, and raises the rest of its body. It then proceeds to strike out in all directions until it meets its prey. When the anterior end of the larva comes in contact with its prey, usually an aphid, the latter is entangled by sticky saliva. The mouth-parts of the larva attach themselves to the aphid, which is lifted up and punctured. Then by backward and forward movements of the mouthparts the entire soft parts of the prey are sucked out.

Under ordinary conditions these larvae feed only on aphids. In the laboratory if syrphid larvae are deprived of food for a period they will eat one another and larvae of other Diptera, such as Cecidomyidae, and even nymphs of leaf-hoppers (jassids). Examples of this characteristic of syrphid larvae are given also by other workers: Verrall (1901) mentions that winged Diptera are attacked by them. Metcalf (1916) records aphids as being 99% of the prey of these larvae, the other 1% being Coccidae, the young of Aleyrodidae, Jassidae, Psyllidae and Membracidae. Krüger (1926) gives several cases of syrphids preying on their own species, on Hymenoptera and on Microlepidoptera.

Syrphid larvae can survive long periods of starvation, provided they are kept supplied with water. A starved larva drinks water avidly. When given water its retracted head and anterior segments expand, its mouth opens and water may be seen passing through the mouth into the gut. The intake of water is helped by the contractions of the dilators of the pharynx, the roof of which may be seen moving up and down. At such a time the anal tubes, which are usually invisible, are alternately put out and withdrawn. A larva which

has been starved for a few days appears comatose and does not attempt to feed even if aphids are brought before it. If, however, it is first given water it will begin to feed in the usual manner.

The female fly lays its eggs on the surface of leaves and on stems of young shoots upon which aphids are present. The process was watched in the cases of *Syrphus balteatus* and *S. luniger*. Eggs are laid singly at short intervals. It was not possible to estimate the number of eggs laid, but Vine (1894) from numerous dissections believes the number to be between 50 and 100, probably nearer the higher figure than the lower.

The eggs are yellowish white, 0·9–1 mm. in length and 0·3–0·46 mm. in width. They are oval in shape and slightly blunt at one end (the micropylar end). The under surface is slightly flattened and the upper exposed surface convex. When examined under a microscope the exposed surface of the egg is seen to possess a distinct pattern, made up of fine elevations of the chorion. These elevations are chalk white in colour, and were considered by Metcalf and Krüger to form a distinct pattern for each species. Eggs of four species were examined; three of these (*S. luniger* (Figs. 1 and 2), *S. balteatus* and *S. ribesii*) showed no difference in their pattern, which consists of elevations running longitudinally; the fourth species (*Platychirus scutatus*) showed a distinct difference in having lozenge-shaped elevations. In all these species the egg hatches after about 48 hr.

All stages of development from egg to adult were followed in *Syrphus luniger* in the laboratory, under as natural conditions as possible. The larvae were kept at room temperature, the leaves changed frequently, an abundant supply of aphids maintained and sufficient moisture given. An adult female, caught on a rose tree, was found to lay eight eggs during a period of 45 min. Twenty-four hours later it died, and subsequent examination showed no eggs in its ovaries.

The eggs commenced to hatch 46 hr. later, the maximum time taken being 55 hr. The actual process of hatching, from the time that the egg shows a slight depression at the sides, and the head of the larva appears through the chorion on the dorsal surface near the micropyle, up to the stage when the larva is free from the egg, takes about 50 min.

Three of the larvae were seen to undergo the first moult approximately 72 hr. after hatching. The process took nearly an hour. The second moult took place 52 hr. after the first, and the puparium was formed after 7–8 days. The adult emerged after 8 days, the whole life history taking 22–23 days. The duration of the different stages is, however, influenced by the amount of available food, moisture and changes of temperature.

Moulted skins are very thin and remain adherent to the surface upon which ecdysis took place. Exuviae of the trachae and buccopharyngeal armature are also shed, and can be seen through the skin. A small longitudinal slit can be seen at the anterior end of the moulted skin, through which the larva has emerged. The process of ecdysis has not been previously observed. Vine (1894)

wrongly believed that no casting of the skin occurred in aphidophagous syrphid larvae. Metcalf (1913) did not see the actual process and says: "Moulting of the larva is inconspicuous, probably consisting of a somewhat continuous process of shedding flake-like pieces."

Defaecation took place only on three occasions in the life history of the larva, when the contents of its hind-gut were emptied. Two of them occurred before the first and second moult respectively, the contents of the gut being of a yellowish colour. The third took place 2 days before the formation of the puparium, the contents of the gut being of a dark colour this time. The larva appeared of lighter colour after defaecation.

The third stage larvae of nearly all species hide themselves in sheltered places before pupation. *S. balteatus* is an exception, and its puparia are found on all parts of the leaves and stems. *Sphaerophoria flavicauda* and *Sph. scripta* prefer young leaves, while the other four species crawl to dried leaves or to the surrounding soil.

At the pupal ecdysis the skin of the fully developed larva is hardened to form a protective case or puparium, in which the pupa develops. This puparium retains all the characters of the larval skin, except that if scales were present on the body of the larva they have now become flattened. To form the puparium the larval skin is inflated on the dorsal side of the anterior end, and shortened along the ventral line. The posterior end of the larva becomes contracted and firmly attached to the surface upon which the puparium is being formed by means of sticky saliva, which may be seen as whitish material at the sides. The mode of dehiscence of the puparium when the image emerges is characteristic for all the species described. It takes place by the separation of two plates (Fig. 31, pl^1 and pl^2; Fig. 46, pl^1), the shape of which is feebly outlined at the anterior end of the puparium, some time before hatching. An opening is formed as a result of this separation, one of the plates being pushed upwards and the other downwards. The upper plate tends to remain attached to the puparium by its posterior margin, and the lower plate by its anterior margin. The point of attachment of the lower plate represents the position of the mouth of the larva. It is interesting to note that the line along which these plates separate is represented by a break in the larval skin (Figs. 54 and 55A). This can be seen if a longitudinal section of the larval skin in the region of the third thoracic and first abdominal segments is examined microscopically. The region is identical with the broad anterior end of the puparium, being parts of the cuticle of the first four body segments of the larva.

Platychirus scutatus hibernates only in the larval stage. Other species hibernate either as larvae or as pupae according to the stage they may be in at the onset of winter. The most commonly found hibernating larva is that of *P. scutatus*, which occurs between November and April on cabbages and Brussels sprouts. As the whole life history of these syrphid larvae occupies no more than about 3–4 weeks, at least three successive generations must occur during one breeding season.

From May to June all stages of *Syrphus ribesii*, *S. balteatus*, *S. luniger*, *Catabomba pyrastri* and *Platychirus scutatus* could be found on roses. During July and August all stages of *Catabomba pyrastri* and *P. scutatus* were obtained from plum trees and thistles, *Syrphus balteatus* and *S. luniger* from a mulberry tree and plum trees and *Sphaerophoria flavicauda* and *Sph. scripta* from cabbages. In September and October all species except *Catabomba pyrastri* were present on cabbages and Brussels sprouts.

It appears therefore that of the species named, only *C. pyrastri* is not present in all stages from May to October, and it may be inferred that in this period at least three generations have been produced, the life history of each being so short.

The occurrence of ichneumonids as parasites of syrphid larvae has been recorded by several authors including Lundbeck, who enumerates some of them. They have also been found in all the species examined by the present author, with the exception of *Syrphus balteatus*, *Sphaerophoria flavicauda* being the species most frequently parasitized. During the months of September, October and November the proportion of larvae parasitized increased considerably, as might be expected. No more than one parasite is usually found within a single larva, but on one occasion a puparium of *Sph. scripta* was found to contain no less than eight parasites. Larval stages of the two commonest parasitic ichneumonids are described in a separate paper.

MORPHOLOGY

Syrphus luniger Meig.

The egg.

The eggs (0·9 × 0·3 mm.) are pure white when laid, but about 24 hr. later become yellowish in colour. At the narrower end of the egg is a brown spot, which is the micropyle (the ectomicropyle of Pantel). The outer surface of the chorion is sculptured with interrupted longitudinal elevations or ridges, which bear a powdery white material, easily displaced by contact and dissolved on immersion in alcohol or xylol. From each main ridge finer branches proceed more or less transversely, to meet similar secondary ridges arising from others. The surface between these ridges is glabrous. Metcalf (1913) describes the arrangement of these elevations as being in oblique lines, and as characteristic of aphidophagous species of Syrphidae, but in the species under investigation this arrangement could not be found. In the eggs of *S. luniger* and others the elevations run longitudinally, the spaces between them being of equal width, except near the micropylar end, where they are shorter and closer together. Sometimes an empty egg-shell gives the impression that the elevations are arranged in oblique lines, by reason of the chorion being depressed in places.

Krüger (1926) found that eggs when about to hatch are increased by about one-third in size. The present writer, on the other hand, observed that if anything there is a slight decrease in width, due to the sides of the egg becoming

depressed. The sharply pointed lips of the larva pierce the chorion a little dorsal to the micropyle many times before the orifice is made large enough to enable the head to be extruded. This break in the chorion is visible only when the lips of the larva are actually protruding. As the larva emerges the chorion contracts, causing the empty shell to appear longer than before.

The eggs are so firmly attached to the surface on which they are laid that they can hardly be removed without breaking the chorion. On one occasion the chorion was completely removed from the embryo which remained enclosed within the vitelline membrane. From this a normal larva emerged the next day, having bitten a slit through the vitelline membrane, similar to that normally made in the chorion. This shows that the chorion is not absolutely necessary for the development of the embryo. It perhaps serves as a projective covering against adverse climatic conditions.

Pantel (1913–14), in his excellent work on the envelopes of the eggs of Diptera, describes the micropylar apparatus as consisting of three main parts:

(*a*) Ectomicropyle, typically consisting of one hole, though more than one may be present, surrounded by a perimicropylar region. It is formed from the chorion.

(*b*) Micropylar conductor, which is of indefinite shape and soft consistency, and projects from the ectomicropyle to the exterior.

(*c*) Entomicropyle, formed from the vitelline membrane, and consisting of a group of cells, in the middle of which is a pore in direct communication with the ectomicropyle.

In the eggs of *S. luniger* and other syrphid larvae, the micropyle which appears as a brown spot, consists of ecto- and entomicropylar plates closely applied to one another. This can be seen if the chorion is completely removed, and the part of the vitelline membrane immediately below the ectomicropyle is laid flat. Ecto- and entomicropyle are similar in structure, both having two pores surrounded by a number of ridges. The former is brown, the latter yellow.

The micropylar conductor was not seen in syrphid eggs. Pantel suggests that the function of this conductor is to protect the micropylar opening and facilitate the entry of the sperms, but he does not say if it disappears after fertilization.

First stage larva.

As in most cyclorrhaphous Diptera, the larva passes through three stages, separated by two moults. A freshly hatched first stage larva (Fig. 4) is about 1·5 mm. long and 0·4 mm. wide at the fourth abdominal segment. It is yellowish white in colour, but after feeding on aphids the contents of the gut appear dark green. It increases rapidly in size, and a definite increase is seen after it has fed on its first aphid. The fat-body of the larva is small and poor in reserve material.

The segmentation of the larva is indistinct, because of the presence of numerous transverse folds and wrinkles in the integument. The pseudocephalon

is very small, and as in all cyclorrhaphous larvae, its anterior portion is divided into two lateral lobes by a median groove (Fig. 5). The greater part of the surface of the pseudocephalon is covered with minute backwardly directed spinules, those on the ventral surface behind the mouth being the most prominent.

On the dorsal surface of the body nine prominent transverse rows of hairs are seen, the first of these belonging to the first thoracic segment, the second to the third thoracic, and the remainder to the first seven abdominal segments. The number of hairs in each row remains the same in the later stages, and will be described with the third stage larva. The eighth abdominal segment has only one spine on either side, and a pair of abdominal spiracles.

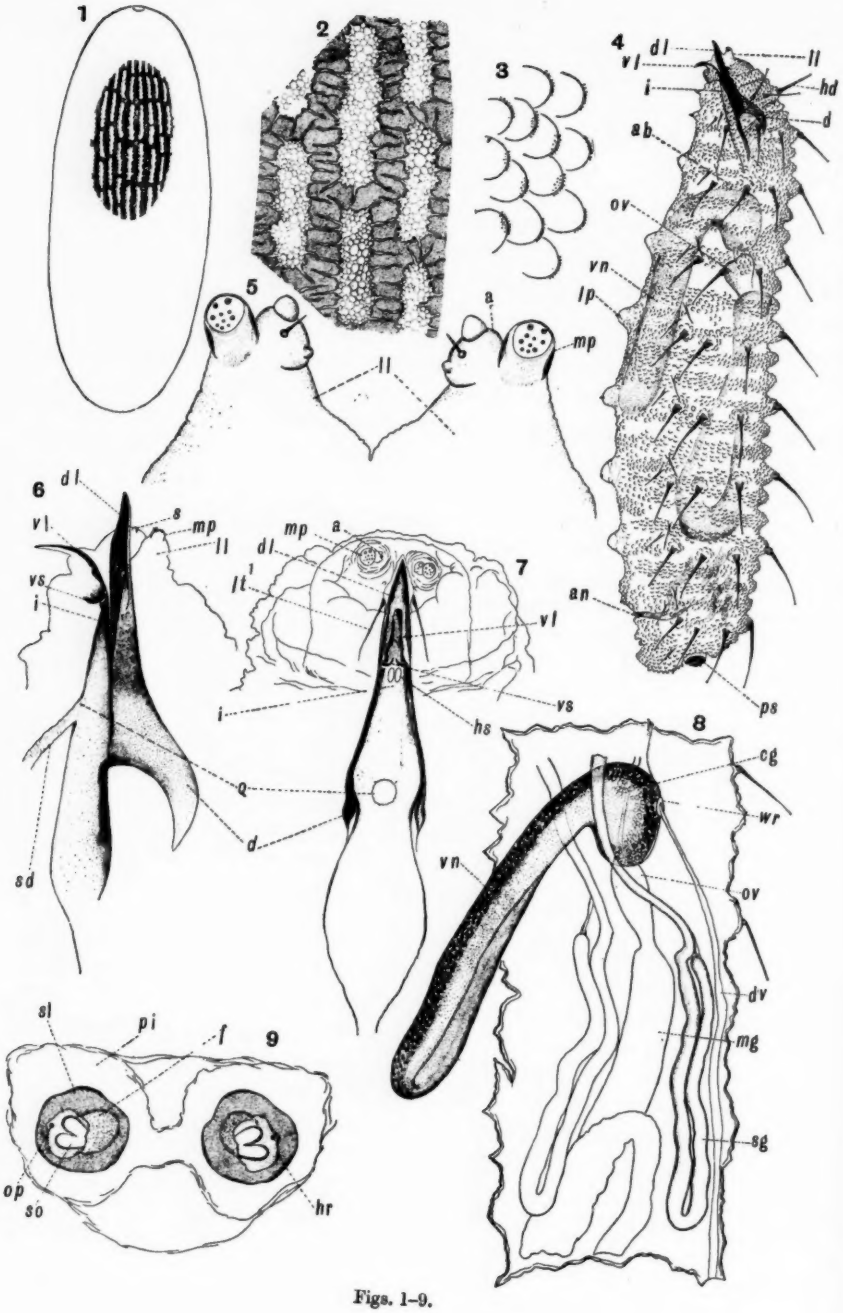
The pseudocephalon and the three thoracic segments are capable of much extension. A transverse row of minute sensillae is present on the ventral surface of the first and the second, but not on the third thoracic segments. The first six abdominal segments have pseudopod-like projections for locomotion (Fig. 4, *lp*) on their ventral surface. These projections are also present on the seventh and eighth segments, but are poorly developed. The anus is present on the ventral surface of the eighth abdominal segment close to the suture dividing the seventh and eighth abdominal segments.

As the whole integument of the larva is colourless and transparent, most of the internal structures can be seen through it. Except for the pseudocephalon and the region of the transverse folds, the whole surface of the larva is covered with small scales. A number of tubercular warts are present on the surface of the dorsal scales (Fig. 3).

Each of the long hairs mentioned is situated on an elevation of the integument (Fig. 4, *hd*) and has two distinct segments, a small basal and a long narrow distal one. The basal segment has a number of minute sensory hairs situated near the commencement of the narrow distal part of the hair, and the distal segment forms a knob at its extremity. The average length of the hairs is 0·16 mm., the hairs of the posterior segment being longer than those of the anterior segments.

The first stage larva is metapneustic, the spiracles being present on the dorsal surface of the last abdominal segment. Each spiracle faces backwards, and is placed on a slight prominence of the integument, surmounted by a pale brown nearly circular plate (Fig. 4, *ps* and Fig. 9). The two plates are fairly wide apart, and each of them has a lighter and more or less rectangular area, on which a pair of spiracular openings (*so*) is present, the partition between the two openings being incomplete. An opening (*op*) of the perispiracular gland is close to the spiracular openings, and two fine hairs are present on each spiracular plate (Fig. 9, *hr*). The spiracular openings communicate with the lateral tracheal trunks through an atrium or felt chamber, which is a very short cylindrical tube. On its inner surface the atrium bears a large number of chitinous hair-like structures (trabeculae).

Mouth-parts. The apex of each of the lateral lobes of the pseudocephalon is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Figs. 1–9.

surmounted by a pair of sense organs lying side by side and partly fused together (Fig. 5). The dorsally situated sense organ, one side of which faces the groove of the head, is the antenna (*a*). It consists of two distinct parts, a small conical apical part and a much larger circular basal one. The basal segment has a thin rounded protuberance and a hair on its ventral surface. The other organ is the maxillary palp (*mp*). It is subcylindrical in shape with strongly chitinized walls. Its terminal flat surface bears about ten sensory papillae, two of which are more prominent than the others. The two organs, antenna and maxillary palp, together have been appropriately called "antenno-maxillary complex" by Keilin (1915). They are partly fused together, but each is independently in communication with its nervous sensory bulb. These two organs are present in all cyclorrhaphous larvae, though not usually so near each other as in the syrphid larvae. The lateral lobes of the pseudocephalon, bearing these two organs, were considered as maxillae by Lowne (1890). Wandolleck (1898) also believed the two organs to be one, which he called the antenna, in spite of having seen the two parts supplied by two different nerve ganglia. De Meijere (1900) in his work on the *Lonchoptera* larva, was the first to point out that the "organ" was the bearer of an antenna and a maxillary palp. Lundbeck (1916) uses the term antenna-like papillae for these two organs.

Anteriorly on either side of the opening of the mouth (Fig. 6) is a small sensory papilla (*s*), the nerve supply of which is derived from the nervous bulb of the maxillary palp. Posterior to each of these sensory papillae is seen the anterior end of a lateral rod (Fig. 7, lt^1) which is a filamentous chitinous structure pale brown in colour projecting backwards into the body cavity of the larva to about the first thoracic segment. The most conspicuous parts of the buccal apparatus are the two sharply pointed dark brown pieces, which are parts of the median dorsal and median ventral lips described below.

Pharyngeal armature (Figs. 6, 7) has a continuous solid chitinous skeleton. It is composed of the following parts:

(1) *The basal or pharyngeal* sclerite, which is very dark and forms dorsal and ventral wings on either side. The ventral side of the sclerite, which forms the floor of the pharynx, is very thin and colourless, especially behind the opening

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Legends to Figs. 1–9.

Syrphus luniger

Fig. 1. Egg. Only a small area of chorion has been drawn to show the pattern. ×61.
Fig. 2. A portion of the chorion of the egg greatly magnified showing details of pattern. ×735.
Fig. 3. Scales from the dorsal surface of the body of first stage larva. ×768.
Fig. 4. Lateral views of first stage larva. ×64.
Fig. 5. Lateral lobes of the pseudocephalon showing antenno-maxillary complex of the first stage larva. ×678.
Fig. 6. Lateral view of cephalopharyngeal skeleton of first stage larva. ×223.
Fig. 7. Ventral view of the same. ×235.
Fig. 8. Dissection of the first stage larva to show the ventral nerve mass. ×86.
Fig. 9. Posterior spiracles of first stage larva. ×2941.

of the salivary duct. The dorsal wings of the two sides form thin, colourless and vertical crests, converging anteriorly, and ending at the tip of the dorsal lip. The posterior darkly chitinized parts of the dorsal wings of the two sides are inclined together and are held in this position partly by a transverse band of muscles seen in the posterior extremities of these wings, and partly by the thin but double hypodermal layer of cells. From the ventral surface of the dorsal wings which form a false pharyngeal roof arise the dilator muscles of the roof of the pharynx.

(2) *Median dorsal and median ventral* lips (thus named by Keilin (1915)) form the mouth proper, and are in direct continuity with the basal part of the skeleton, and are pointed blade-like structures. It has been shown by Keilin that these can be homologized with the labrum and labium of other insects. My observations confirm Keilin's view that the dorsal lip is continuous with and forms part of the chitinized external terminal part of the suprapharyngeal sac. The ventral lip is merely a strongly chitinized forward prolongation of the anterior floor of the pharynx (hypopharynx). The point of commencement of the ventral lip from the basal skeleton is marked by a pair of ventral saucer-like structures (*vs*) projecting into the body cavity. At this point the lip is very flexible, and bends most when the larva opens its mouth. The median dorsal lip always remains in a straight line with the rest of the skeleton and is very rigid.

(3) *The intermediate or hypopharyngeal* part is completely absorbed in the ventral lip. The region which represents it is the floor of the mouth (Fig. 7, *i*), between the opening of the salivary gland and the flexible region of the ventral lip. A pair of colourless oval areas enclosing special sense organs (*hs*) described later (*Platychirus scutatus*), are present on the hypopharynx near the origin of the ventral lip.

Keilin states that the lateral rods appeared only in the third stage larva. I have found one pair (Fig. 7, lt^1) of them present in the first stage larva, the other rods arising from the pharyngeal skeleton being absent.

The most striking feature in the anatomy of the first stage larva is the size of its ventral nerve mass (Fig. 8, *vn*). This is about 0·7 mm. long and 0·1 mm. broad, and is about one-half the total length of the larva. The Weismann's ring (*wr*) is situated on the anterior dorsal part of the cerebral ganglia, not on the posterior dorsal part as in the second and third stages. The rest of the anatomy is essentially similar to that of the third stage larva.

Second stage larva.

Soon after the first moult, the second stage larva is 4·4 mm. long and 0·9 mm. broad at the fourth abdominal segment. When fully developed it attains the size of the third stage larva. The larva is more opaque than in the first stage, but its internal organs are still visible by transmitted light. The fat-body is conspicuous under the skin of the dorsal side and is yellowish in colour. The dorsal surface of the skin differs from that of the first stage in having groups of

brown scales. The tubercular warts seen on the scales of the first stage are indistinct. The sensory hairs are paler and shorter and are similar to those of the third stage. The ventral surfaces of the first and second thoracic segments have a transverse row of fine hairs instead of papillae. The hairs of the second segment are longer than those of the first and have a yellowish colour.

The larva has become amphipneustic, a pair of functional spiracles (Fig. 11, *as* and Fig. 12) being present on the first thoracic segment. Each spiracle consists of a brownish papilla projecting from a pit on the dorso-lateral part of the segment. It has a wide circular opening facing backwards, the posterior margin of which is very faint. The opening communicates with the anterior end of the main tracheal trunk of that side through a very small felt chamber.

The spiracular plates of the posterior abdominal spiracles are still wide apart, but each plate has three distinct openings on its surface and a spiracular scar (*sr*) of the preceding stage on its inner surface. There are four openings of the perispiracular glands, one of which is double, the two parts being connected by a short canal. A fine hair is present near the main opening of each perispiracular gland (Fig. 13).

Buccopharyngeal armature (Figs. 10 and 11). The dorsal and ventral lips differ from those of the first stage larvae in having strongly chitinized lateral margins. The most important changes which have taken place in this stage are: (*a*) Development of two comb-like sclerites (*cs*) with anteriorly directed teeth, on either side of the mouth opening. These scelerites are not connected with the ventral lip and seem to have originated from the integument of the pseudocephalon.

(*b*) The posterior part of the ventral lip at its junction with the hypopharynx is greatly thickened.

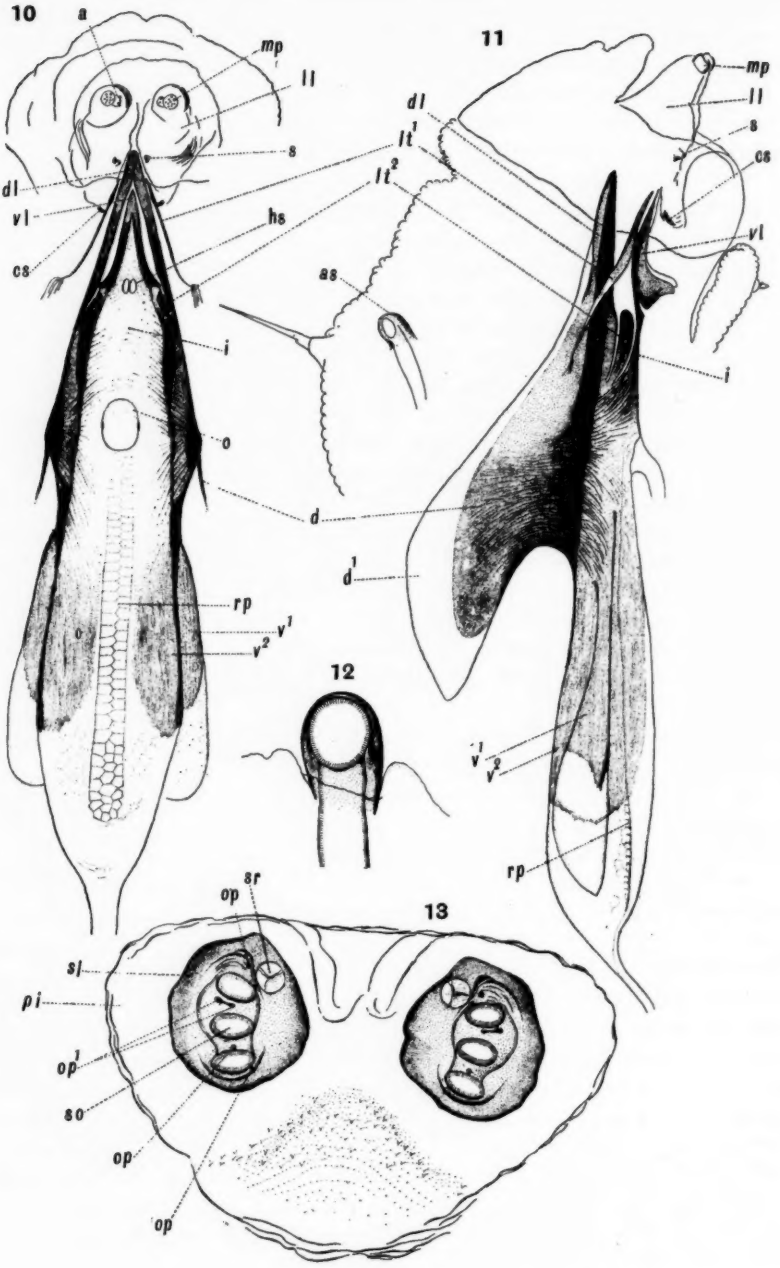
(*c*) A lateral rod (lt^2) has appeared, which arises from the skeleton at the angle formed by the dorsal and ventral lips.

(*d*) The ventral basal plate (v^2) has developed an outer wing (v^1).

(*e*) The roof of the pharynx has become strongly chitinized along the median axis and has polygonal markings on its surface (*rp*).

Third stage larva.

Soon after the second moult the third stage larva is 6 mm. long and 1 mm. broad at the fourth abdominal segment and attains a length of 11·0 mm. and width of 2·5 mm. before the formation of the puparium. The integument of the larva is opaque and its colour varies from that of straw to dirty brown, with groups of black spots on the dorsal surface of the segments (Fig. 14). The heart line seen in the mid-dorsal region is interrupted at intervals by the fat-body. The pseudocephalon is surrounded by a ring of ten sensillae on its dorsal and lateral sides. On the ventral side below the mouth are two sensillae fused together on either side, the labial sensillae (Fig. 15, *ls*). The segmentation of the body is ill-defined, as in the first two stages, but the abdominal segments can be distinguished from the three thoracic by the presence of the locomotory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Figs. 10–13.

projections and the larger number of dorsal hairs in all segments except the last.

The first thoracic segment has a transverse row of six hairs just behind the spiracles. They are absent from the second thoracic segment and eight hairs are present on the third thoracic segment. The first abdominal segment has sixteen hairs, of which only twelve are seen on the dorsal surface, the remaining two of each side being placed laterally. Twelve hairs are present on the second to seventh segments, the two middle hairs being placed a little anterior to the others. The eighth segment has only two hairs, one laterally on either side. The eighth abdominal segment also bears the two posterior spiracles, which are very prominent structures in this stage. Each dorsal hair is situated on a conical projection of the skin and consists of a rounded basal and a long terminal part. A pit containing refractile bodies is present on the basal part of the hair (Fig. 16, *st*). The average length of a hair is about 0·17 mm., nearly the same as in the first stage larva.

The ventral surface of the first and second thoracic segments each has a transverse row of ten dark hairs. The four submedian hairs of the row of first segment are shortest, and the two outer ones are the longest. In the second thoracic segment the hairs are longer, and, as in the first, the four middle ones are the shortest. The ventral surface of the third segment is devoid of hairs.

The ventral surface of the abdominal segments is characterized by the great development of locomotory projections which are arranged in two groups of three, one group on each side of the first six abdominal segments. On the seventh and eighth segments they are not so conspicuous and are arranged on each in a transverse row, anterior to the anus in the seventh, and along the posterior border on the eighth segment.

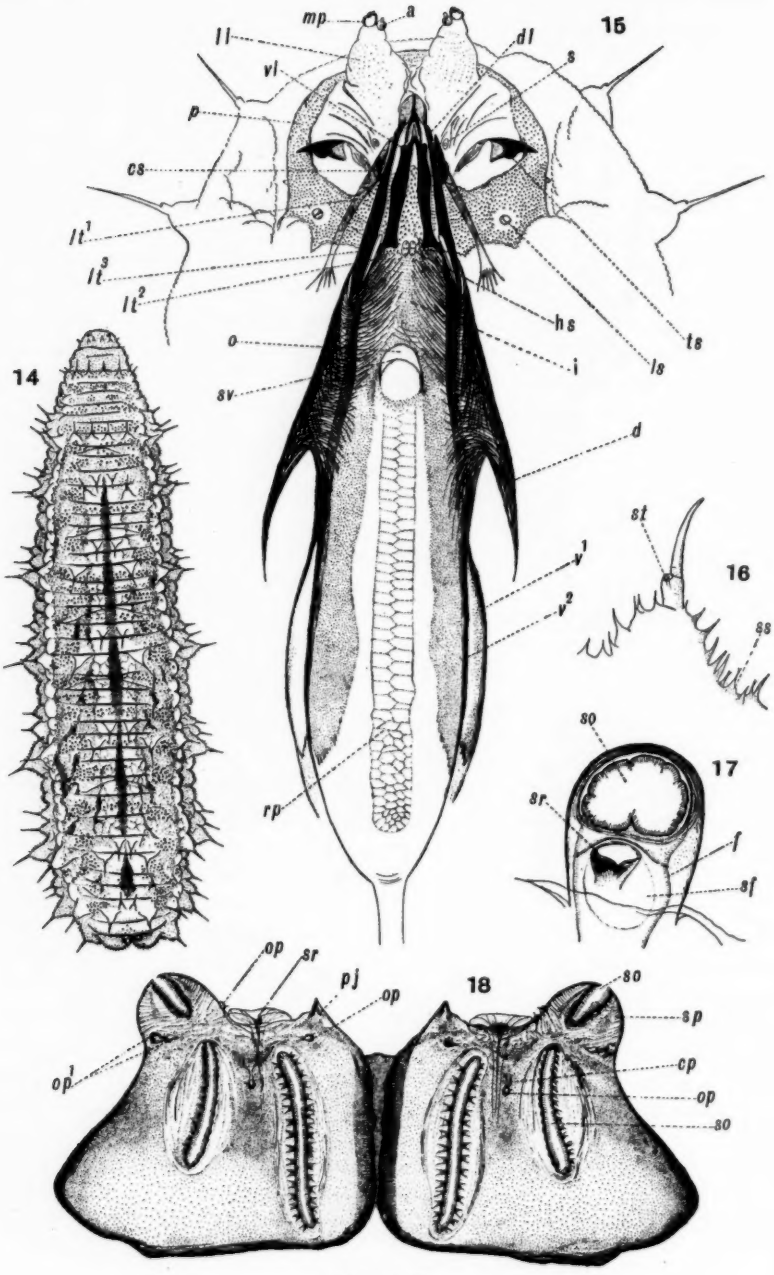
The whole integument of the larva is covered by brownish spinules. Some of these spinules are situated very near together, and have wide circular bases and forked ends (Fig. 16, *as*) so that groups of them give the appearance of the black spots on the surface of the larva described above.

The larva is amphipneustic. The prothoracic spiracle (Fig. 17) has a single opening with an uneven outline, due to the projections of membrane around the opening. The most posterior of these projections is the longest. A spiracular scar is seen on the posterior wall of the spiracular papilla, and is connected by chitinous strands to another scar beneath it on the wall of the felt chamber. The posterior spiracles (Figs. 18, 19 and 20) have a characteristic shape. They arise from the cuticle of the eighth abdominal segment, are strongly chitinized and are united together in the medio-dorsal line. Each spiracular opening, of

Legends to Figs. 10–13.

Syrphus luniger

Fig. 10. Ventral view of cephalopharyngeal skeleton of second stage larva. ×162.
Fig. 11. Lateral view of the same. ×175.
Fig. 12. Prothoracic spiracles of second stage larva. ×544.
Fig. 13. Posterior spiracles of second stage larva. ×240.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Figs. 14–18.

which there are three in each spiracle, is elongate and slit-like and is borne on a separately raised prominence. Submedially and close to the spiracular scar of each spiracle is a conspicuous conical projection (*Pj*). The perispiracular glands have four openings to the surface, of which one (*op'*) is double. On the surface, each of these openings leads into a short channel, which widens gradually in its course towards the centre of the spiracle.

The buccopharyngeal armature (Fig. 15) is even more chitinized in this stage. In the mouth-parts, in addition to the structures described in the first two stages, there are a pair of triangular sclerites with hooked extremities (*ts*), situated on either side of the mouth and a pair of lateral (lt^3) rods arising from the angle of the dorsal and ventral lips. The maxillary palp of the second and third stages differs from that of the first stage in being larger than the antenna. The structure of these two remains the same in all three stages, except for a slight thickening which appears on the inner side of the antenna in the third stage. The roof of the pharynx is very like that of the second stage, only more strongly chitinized.

It is convenient at this point to enumerate the total number of structures forming the mouth-parts of the third stage larva and to mention their action during feeding. This number is constant in all the species described, the difference between them being one of shape and degree of chitinization, and is best shown by figures. These structures may be divided into two groups, viz. (*a*) those which are derived from the pharyngeal skeleton and (*b*) those not so derived.

(*a*) The first group consists of the following parts:

(1) Dorsal and ventral lips (*dl* and *vl*).

(2) Two lateral rods arising from the angle formed by the dorsal and ventral lips at either side of the mouth (lt^2, lt^3).

(3) Two oval areas enclosing special sense organs in the anterior part of the hypopharynx—the hypopharyngeal sense organs (*hs*).

(*b*) The second group comprises:

(1) Antenno-maxillary complex, situated on the lateral lobes of the pseudocephalon (*a* and *mp*).

(2) Two buccal sensillae (*s*).

(3) A pair of outer lateral rods (lt^1).

(4) Two comb-like sclerites (*cs*).

(5) A pair of triangular hook like sclerites (*ts*).

The method of feeding is as follows: When the larva has met its prey, its sharply pointed lips pierce the body of the latter. The mouth opens by the

Legends to Figs. 14–18.

Syrphus luniger

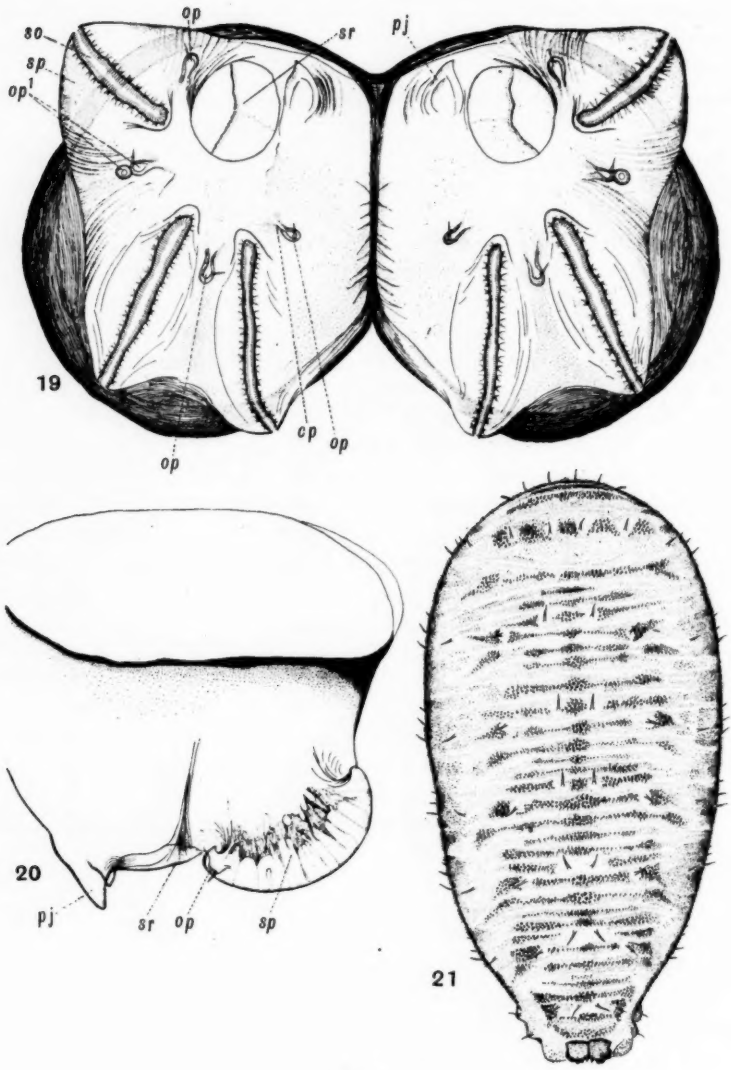
Fig. 14. Dorsal view of third stage larva. ×9.

Fig. 15. Ventral view of cephalopharyngeal skeleton of third stage larva. ×112.

Fig. 16. Sensory hair of third stage larva. ×85.

Fig. 17. Prothoracic spiracle of third stage larva. ×315.

Fig. 18. Posterior spiracles of third stage larva seen from the posterior side. ×243.



Syrphus luniger

Fig. 19. Facial view of posterior spiracles of third stage larva. ×237.
Fig. 20. Dorsal view of posterior spiracles of third stage larva. Only one side shown. ×215.
Fig. 21. Puparium. ×10.

downward movement of the ventral lip, and the larva commences to suck out the soft parts of the prey. The outermost lateral rods (lt^1), which are not connected to the main skeleton, help the process by means of movements in a horizontal plane. The other lateral rods, which are connected to the main skeleton, act merely as supports to the side of the mouth. The larva penetrates deeper and deeper, aided by the comb-like and triangular sclerites, until the whole pseudocephalon is buried in the body of the prey.

The ventral nerve mass (*vn*) is 1 mm. long and 0·3 mm. broad, and is one-sixth the whole length of the larva. Its posterior end is narrower than its anterior.

The puparium.

The puparium (Fig. 21) when completely formed is 7·5 mm. long and 3·8 mm. broad. Although changed into a hard capsule, with all larval folds obliterated, the skin retains the dirty brown colour of the larval skin with groups of black spots on the dorsal surface. It is oval with a narrow posterior end, which bears the posterior spiracles. The external horn-like thoracic spiracles commonly seen in this stage of cyclorrhaphous Diptera are absent, as in all the puparia dealt with in this paper, with the exception of *Platychirus scutatus*.

The following characters are common to all the species described here and descriptions of them will therefore not be given:

(1) A flattened ventral surface and a convex dorsal surface, with a narrow anterior and a broad posterior extremity.

(2) The segmentation masked by secondary folds.

(3) The pseudocephalon covered with backwardly directed hooklets and divided by a median groove into two lateral lobes, each lobe bearing the antenno-maxillary complex. It is partly surrounded dorsally and laterally by an incomplete ring of ten sensillae. On the ventral surface two sensillae are fused on each side to form the labial sensillum.

(4) The posterior end of the last abdominal segment bears four lobes.

(5) All third stage larvae are amphipneustic.

(6) Two prothoracic spiracles, which are brownish in colour, conical, strongly chitinous, and have a single opening.

(7) Two posterior spiracles, placed on a projection of the skin in the eighth abdominal segment. They are fused medio-dorsally, each having three spiracular openings.

(8) Both spiracles (prothoracic and posterior abdominal) have spiracular scars of the previous stage, and chitinous strands travel from them to scars on the wall of the felt chamber.

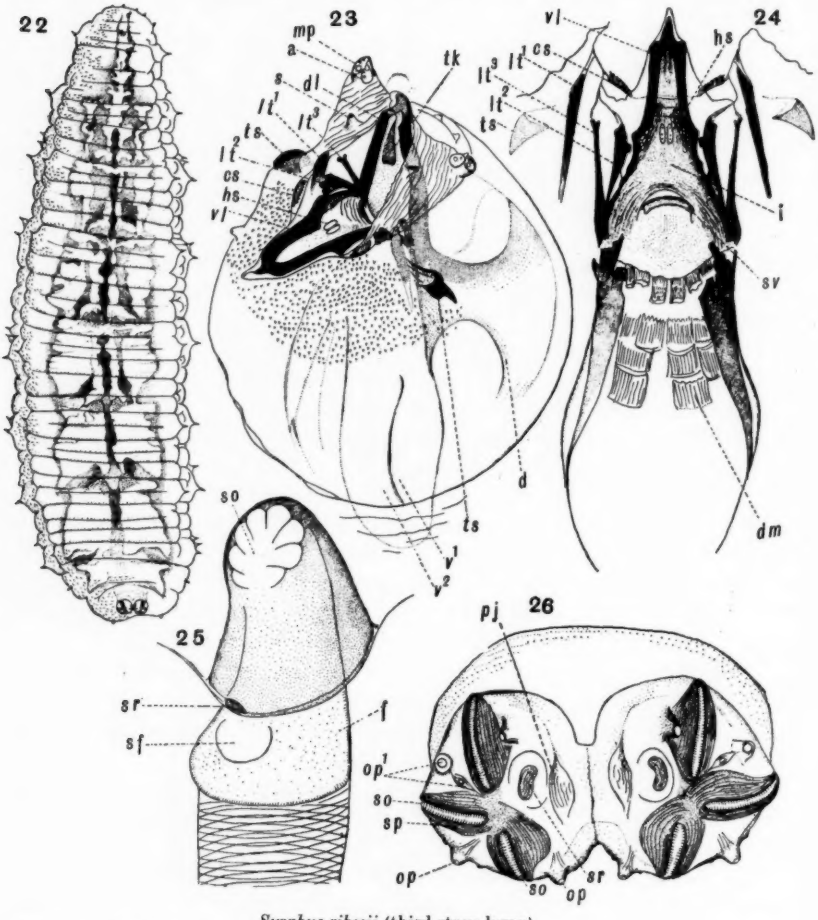
(9) Four openings of the perispiracular glands on the posterior spiracles, one of the openings being double.

(10) The common characters in the mouth-parts mentioned already.

(11) Nine transverse rows of hairs or papillae present on the dorsal surface of the body of the larvae.

Syrphus ribesii Linne

The fully developed third stage larva is 12 mm. long with pseudocephalon retracted, and 3 mm. wide at the fifth body segment. The colour of the larva varies from yellow to pink. It is opaque as a result of the large amount of fat-body, which is arranged as shown in Fig. 22, and is characteristic of this



Syrphus ribesii (third stage larva)

Fig. 22. Dorsal view of the larva. ×8.
Fig. 23. Open mouth of the larva showing mouth parts. ×95.
Fig. 24. Cephalopharyngeal skeleton seen from the dorsal side with the upper lip removed. ×90.
Fig. 25. Prothoracic spiracle. ×325.
Fig. 26. Posterior spiracles. ×94.

species. The fat-body is usually yellowish white in colour, but is pink in the region of the dorsal vessel. The relative amount and depth of the pink colour varies in different specimens.

The transverse row on the dorsal surface of the first abdominal segment has fourteen hairs, in contrast to *S. luniger* which has sixteen. There is one sensillum on either side representing the absent hairs. The number of hairs on other segments is the same as in *S. luniger*. Each hair is mounted on a small elevation, and is about 0·095 mm. long: the hairs of the first few rows tend to be shorter and finer. The ventral surface of the first thoracic segment has a transverse row of ten sensillae, and that of the second thoracic segment has three hairs on either side and four sensory papillae in a transverse row. The entire surface of the integument is covered with minute colourless scales. Well-developed locomotory projections are present on the ventral surface of the abdominal segments. There are four of these in each segment and they are arranged two on either side. There is a sensory papilla in the centre of each projection.

The prothoracic spiracles are conical, the spiracular opening of each being incompletely divided by fine marginal projections except in the posterior part, where the margin is faint and colourless (Fig. 25). The posterior spiracles are a pair of tubercles fused medially (Fig. 26), reddish brown in colour and surmounting a common tubular projection. The openings of spiracles and perispiracular glands are situated on raised prominences. Neither hair nor channels are present in connexion with the opening of perispiracular glands. The projection situated submedially close to the spiracular scar is less raised than in *S. luniger* and not conicle (Fig. 26, *pj*).

Fig. 23 represents the pseudocephalon of the larva with the mouth open and shows the exact relation and position of the various parts of the buccopharyngeal armature. A well-defined thickened brown area is seen on the anterior part of the roof of the upper lip (*tk*). This thickening is present in varying extent in all the species. The terminations of the lateral rods are characteristic for this species (lt^1, lt^2, lt^3). The roof of the pharynx is very feebly chitinized, and the brown longitudinal area found in *S. luniger* is not present. In Fig. 24 the upper lip has been removed, and the ventral is seen, with the opening of the common salivary duct and the origin of the lateral rods from the skeleton.

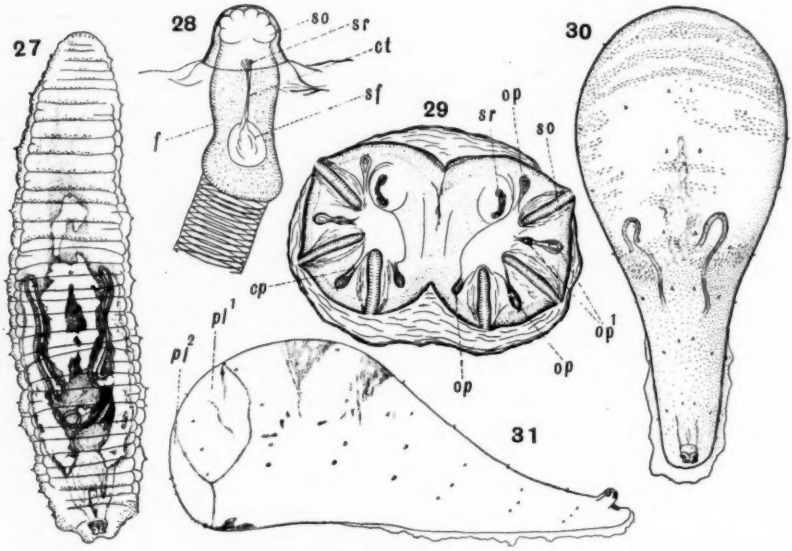
The puparium is 7 mm. long and 3·6 mm. broad. When freshly formed it has the colour and pattern of the larva. Later it is similar in appearance to that of *Catabomba pyrastri*.

Syrphus balteatus De Geer

Mik (1898) correctly described the puparium of this species as being drop-like, white at first and brown later. The adult hatched from it after ten days. Krüger (1926) gives a brief description of the external appearance of the larva. The present writer agrees with his statement that it does not fall on the earth

to form a puparium. Although Lundbeck (1916) says that this species has only one generation and Krüger states it has two, at least three generations have been found to occur in a year at Cambridge.

The fully developed third stage larva (Fig. 27) is about 11 mm. long with its head and thoracic segment retracted, and 2·5 mm. wide at the widest part. The integument is thin, shiny and transparent, and is covered with minute scales. The contents of the anterior part of the mid-gut are green and so give the anterior part of the larva the appearance of being green also. The five lobes of the fat-body are arranged in a definite pattern, one being situated in



Syrphus balteatus (third stage larva)

Fig. 27. Dorsal view of the larva. ×7.
Fig. 28. Prothoracic spiracle. ×171.
Fig. 29. Posterior spiracles. ×90.
Fig. 30. Dorsal view of the newly formed puparium. ×10.
Fig. 31. Lateral view of 2 days' old puparium. ×10.

the centre of the third body segment and the others between the fourth and seventh body segment. They are white, except the two lying between the malpighian tubes, which are often pink in the centre. Two orange-coloured loops of the malpighian tubes are seen among the lobes of the fat-body. The black hind-gut is seen at the posterior end of the larva.

There are three very small papillae on either side of the first and second thoracic segments ventro-laterally. First abdominal segment bears twelve hairs on the dorsal surface and four sensory papillae, two on either side. The number of hairs on other segments is the same as in first two species. Each

hair is 0·038 mm. long, and is not placed on an elevation. There are no locomotory projections on the ventral surface of the abdominal segments, but four small sensillae, two on either side, are present on each segment.

The opening of each prothoracic spiracle (Fig. 28) is incompletely divided by six marginal projections, five on the anterior and one on the posterior margin. A spiracular scar is found at the base of the spiracle, and is connected to the base of the felt chamber by chitinous strands. The tubular projection on which the posterior spiracles are placed is very short and spiracular openings are only slightly raised above the surface (Fig. 29). All the openings of the perispiracular glands lead into channels and hairs are absent. The openings are prominent but not much raised above the surface. The spiracular scar is of a characteristic shape (*sr*).

The buccopharyngeal armature is very like that of *Catabomba pyrastri*, except that its triangular sclerites have blunt extremities, and the roof of the pharynx is very thin and does not show a strongly chitinized medial longitudinal area.

The puparium is club-shaped, 6·7 mm. long with a maximum width of 3 mm. When freshly formed it is white and transparent (Fig. 30), but after two days it shows two brown triangular areas on the dorsal surface (Fig. 31).

Catabomba pyrastri Linne

The first record of this larva is made in *Les Insectes*, 1878, where an illustration of it is given and mention made that it lives on aphids. Bloomfield (1900) describes this species as being bred from a Lepidopterous pupa, *Plusia iota*. Aldrich points out this mistake and says that he reared this species from a larva which fed on grain aphids. Metcalf (1913) states that from the shape of the puparium it can be seen that the larva is essentially similar to aphidophagous larvae. It is now found without doubt to be aphidophagous.

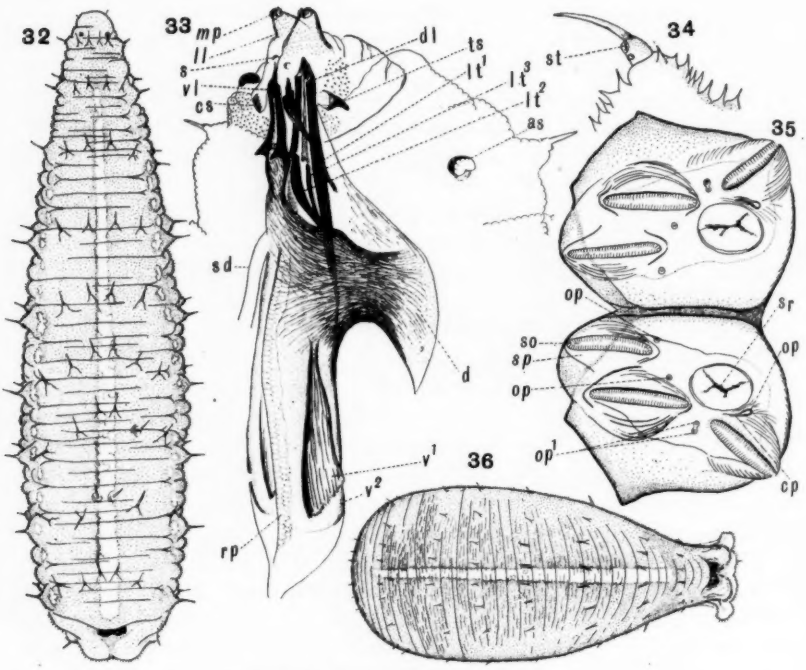
When fully developed the third stage larva (Fig. 32) is 16 mm. long and 4 mm. wide at the fourth abdominal segment. The length is slightly increased during movement. In colour it is green, with a white mid-dorsal longitudinal line. The dorsal surfaces of the lateral lobes of the pseudocephalon have a brownish colour. The number and arrangement of hairs forming the nine transverse rows on the body segments and that on the ventral surface of the first and second thoracic segments is the same as that of *S. luniger*. A single hair is also present on either side of the eighth abdominal segment. Each dorsal hair is 0·17 mm. long and is situated on a prominence of the integument (Fig. 34). The spinules covering the whole integument are all of the same size and are arranged in a uniform manner. Their ends are not forked.

The opening of the prothoracic spiracles is semicircular, and its margin dentated by six marginal projections, five on the anterior and one on the posterior part (Fig. 33, *as*). The posterior spiracles (Fig. 35) are placed on a pair of strongly chitinized tubercles, fused medially. There are no hairs near the openings of the perispiracular glands, and only one of them leads into a

channel. The openings are very small and not much raised from the surface while each of the spiracular openings is distinctly raised.

The buccopharyngeal armature is essentially similar to that of *S. luniger*, the differences being mainly of size and shape of the component parts, shown in Fig. 33.

The puparium (Fig. 36) is 9 mm. long and 4 mm. wide. When newly formed it is brownish green in colour, and has a white longitudinal line on the dorsal surface. Later it becomes pale brown and the longitudinal line disappears.



Catabomba pyrastri (third stage larva)

Fig. 32. Dorsal view of the larva. ×6.
Fig. 33. Cephalopharyngeal skeleton. ×67.
Fig. 34. Sensory hair from the dorsal surface of the body of the larva. ×94.
Fig. 35. Posterior spiracles. ×91.
Fig. 36. Puparium. ×6.

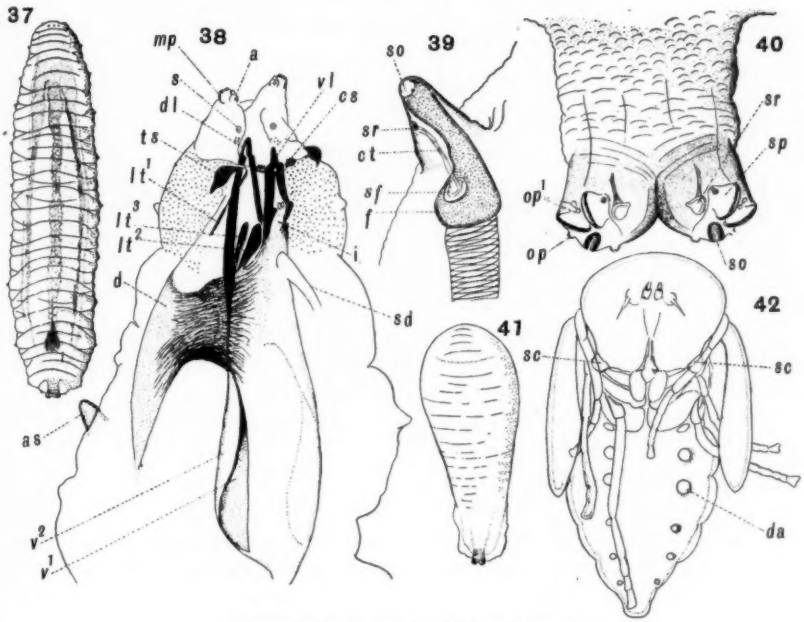
Sphaerophoria flavicauda Zett.

Verrall (1901) says that very little is known of the metamorphosis of this species. He was convinced that it does not feed on aphids, but gives no reason for his conviction. He also mentioned an association between this species and the garden asparagus. During the course of this work, however, the present

writer has witnessed the feeding of the larvae on aphids and, moreover, that they are carnivorous may be inferred from the structure of the pharyngeal skeleton.

The fully developed third stage larva is 8 mm. long and 1·8 mm. wide. It is light green in colour and bears two long white streaks on either side. The skin is transparent and covered with minute scales (Fig. 37).

The first thoracic segment has six papillae dorsally, three on either side, but lacks them on the ventral surface. The second thoracic segment has also



Sphaerophoria flavicauda (third stage larva)

Fig. 37. Dorsal view of the larva. ×6.
Fig. 38. Cephalopharyngeal skeleton. ×94.
Fig. 39. Prothoracic spiracle. ×188.
Fig. 40. Posterior spiracles. ×116.
Fig. 41. Puparium. ×6.
Fig. 42. Pupa of *Sph. scripta* enclosed within the prepupal membranous cuticle. ×7.

three papillae on either side, but four minute papillae on its ventral surface. On the dorsal surface of the third thoracic segment there are two minute blunt hairs medially and three papillae on either side. The dorsal surfaces of the first to the seventh abdominal segments have two short hairs medially and five papillae on either side. The eighth segment has a single papilla on each of the outer lobes. The ventral surface of each of the first seven abdominal segments has three locomotory projections on either side, which are poorly developed.

Each projection bears a minute papilla. The ventral surface of the eighth segment has one papilla on each of the inner posterior lobes. The prothoracic spiracles are borne on a pair of conical projections, and have each a circular opening interrupted by five marginal projections (Fig. 39). The posterior spiracles (Fig. 40), are situated on a prominent backwardly directed tubular projection, which is 0·44 mm. long and 0·34 mm. wide. The perispiracular glands open on slight prominences and none of them leads into channels nor are any hairs present. The spiracular scar is heart-shaped.

In the buccopharyngeal armature no longitudinally thickened area is seen in the roof of the pharynx (Fig. 38), and the lateral rods (lt^2 and lt^3) are very short.

The puparium (Fig. 41) is 5·3 mm. long and 2 mm. wide. When mature it is pale brown in colour.

Sphaerophoria scripta Linne

The third stage larva is very similar to that of *Sph. flavicauda*. It differs mainly in being larger in size, being 9 mm. long and 2·2 mm. wide. It is green, with a pair of longitudinal white streaks more marked than in *Sph. flavicauda*. The arrangement and number of papillae and hairs on different segments of the larva is the same as in *Sph. flavicauda*.

The posterior spiracles are situated on a tubular projection which is shorter than that of *Sph. flavicauda* and is 0·41 mm. × 0·37 mm. The openings of the perispiracular glands are level with the surface.

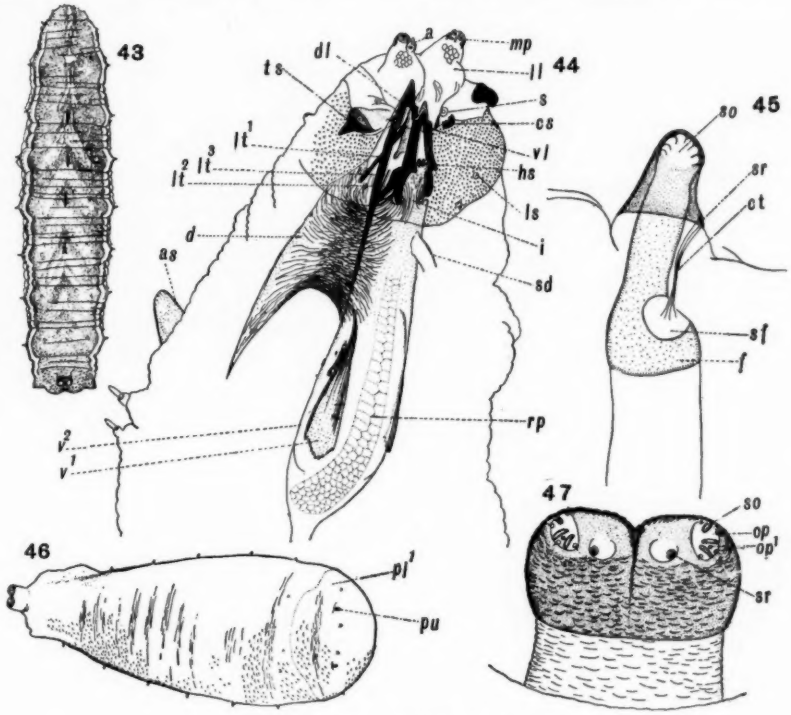
The puparium is 7 mm. long and 2 mm. wide, and is similar in appearance to the puparium of *Sph. flavicauda*.

Platychirus scutatus Meig.

The larvae of this species are of interest because the genus to which they belong has not hitherto been recorded as aphidophagous. Verrall (1901) describes the larva as having been bred from rotten fungi. Folsom (1909) suspected their aphidophagous nature from the presence of adults of *Platychirus quadratus* among clover aphids. Metcalf (1917) bred larvae of *P. scutatus* which he fed on aphids. Krüger (1926) first found larvae of *P. scutatus* while fishing through a pond with a plankton-net and later from *Sambucus* among aphids. From their habits and morphology the present writer is convinced that this species is aphidophagous.

The third stage larva is 8·9 mm. long and 2 mm. wide. It is green and bears oblique pinkish white streaks directed forwards and meeting in the mid-dorsal line (Fig. 43). There are some white spots on the sides. The whole body is covered with scales. The first thoracic segment has six hairs on the dorsal and three sensory papillae on the ventral surface. The second thoracic segment has no hairs on the dorsal surface, and on the ventral surface three sensory papillae, as in the first segment. The dorsal surface of the third segment has eight hairs and the ventral surface none. The first seven abdominal segments

have each a transverse row of ten hairs on the dorsal surface, and a lateral sensory papilla on either side. The last segment has one sensory hair on either side of its posterior margin. Each hair is short, blunt, 0·47 mm. long, and is situated on a slight elevation of the integument. Locomotory projections are absent from the ventral surface, but their position is marked by three sensory papillae on either side of the mid-line. The two middle papillae are smaller



Platychirus scutatus (third stage larva)

Fig. 43. Dorsal view of the larva. ×8.
Fig. 44. Cephalopharyngeal skeleton. ×97.
Fig. 45. Prothoracic spiracle. ×236.
Fig. 46. Puparium. ×10.
Fig. 47. Posterior spiracles. ×63.

than the others. The prothoracic spiracles (Fig. 45) are situated on conical projections, the opening of each having seven marginal projections anteriorly, the posterior margin being very thin and without projections. The posterior spiracles (Fig. 47) are situated on a tubular prominence, the spiracular openings being level with the surrounding surface, which is colourless and shiny, There are four hairs, one near each opening of the perispiracular glands. The double opening (op^1) of the perispiracular gland, unlike those of other species,

has no superficial connexion between the two parts. All the openings of perispiracular glands are level with the surface and no channels lead from them.

The buccopharyngeal armature (Fig. 44) shows one of the lateral rods (lt^2) partly fused with the ventral lip. The roof of the pharynx has a well-marked thickened longitudinal median area (*rp*).

The puparium (Fig. 46) is 5·4 mm. long and 2·5 mm. wide, and has horn-like pupal spiracles (*pu*) which project from the broad anterior part.

Pupae in general

The pupae of all the species described above are coarctate. In general appearance a pupa of any of the above species shows all the essential features of the imago; the differentiation into head, thorax (with its legs, wings and halters) and abdomen is complete. The cuticle of the pupa is very thin and transparent, and the corresponding parts of the developing imago can be clearly seen within it (Fig. 42).

On dissecting the puparia, which had been preserved in alcohol, the author found traces of a substance, the colour of which varied from white to pale brown, covering the cuticle of the pupa in many places. At the beginning of the work the author was under the impression that this substance was the remains of a prepupal stage, which had been described by Snodgrass in *Rhagoletis pomonella*, and Lowne in the blow-fly. The latter called the stage pronymph. The existence of this stage was also pointed out by Lubbock in Lonchoptera but was disproved by De Meijere.

After dissecting a large number of puparia (at different stages of development) of the species dealt with in this paper, the present author came to the conclusion that no prepupal stage existed. The substance seen covering the various parts of the cuticle is nothing but the solidified exuvial fluid. If a puparium is dissected with a living pupa inside it, the milky exuvial fluid can be seen to flow out and no substance is found on the cuticle. In addition to this when the fully developed imago comes out of the puparium, only one exuvium is found within the latter. According to Snodgrass there should be two if a prepupal stage were present.

The structures characteristic of the pupa are the following:

(1) On the head of the pupa, just below the region of the compound eyes, on each side is a colourless subocular lobe, which is disk-like and backwardly directed (Fig. 42, *sc*). Similar lobes were found by Künckel d'Herculais in Volucellinae and described by him as being peculiar to syrphid pupae. Snodgrass also found them in *Rhagoletis pomonella*. Subocular horns of an adult fly have been described by Saunders in Elaphomyia.

(2) On the anterior part of the dorsum of the thorax (mesonotum) is a pair of prominent oval swellings (Figs. 48–53, *sw*).

(3) On the ventral surface of each of the abdominal segments is a pair of disk-like swellings (Fig. 42, *da*).

It is suggested that the swellings are responsible for forming the shape of the puparium of Syrphidae and help in the hatching of the puparium. The subocular lobes and the swellings on the dorsum of the thorax would aid in expanding the larval skin of the anterior body segments. On the third or fourth day after the formation of the puparium, its posterior narrower part is always seen to be empty, the pupa having been pushed forward after detachment from the larval cuticle at this end. It is therefore reasonable to believe that this movement forward of the pupa was brought about by the ventral abdominal swellings which served as pseudopods.

Spiracles (Figs. 48–53)

The larval spiracles cease to function soon after the puparium is formed. The main tracheal trunks attached to the larval spiracles are seen lying broken and collapsed between the pupal cuticle and the puparium.

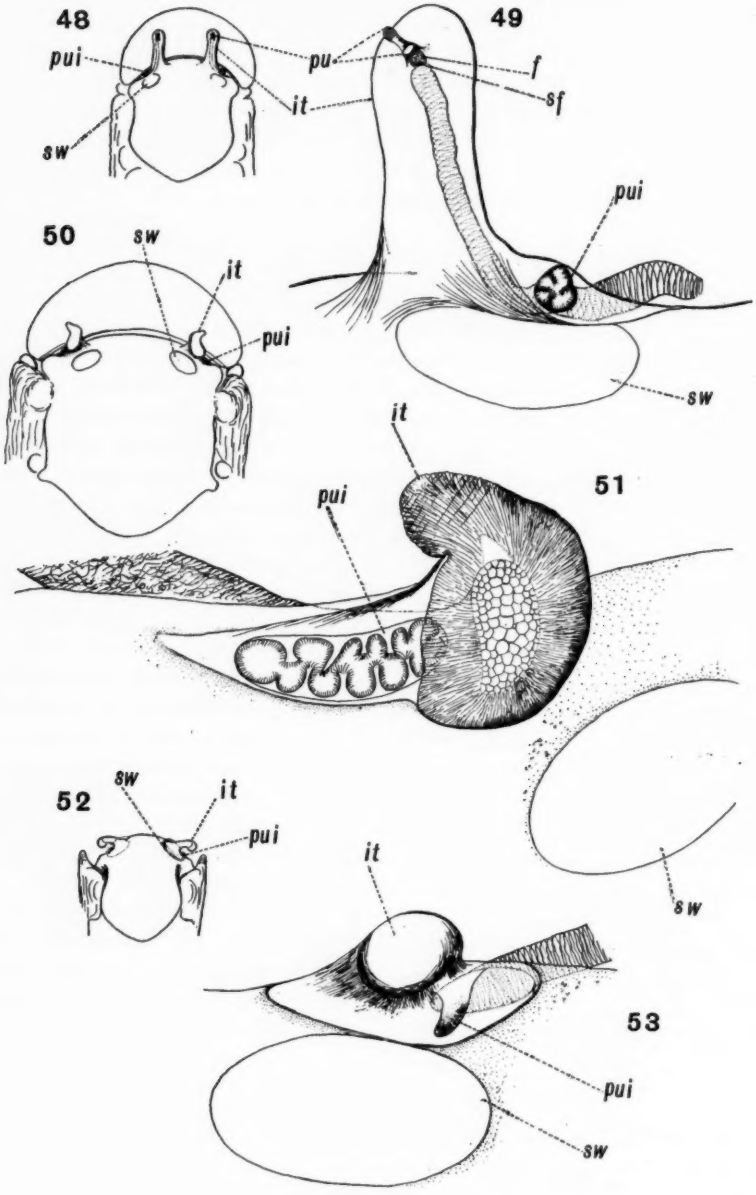
A pair of special processes are seen to arise from the anterior margin of the dorsum of the thorax, just in front of the swellings. These processes are blind in all the species and remain inside the puparium except in *Platychirus scutatus*, in which they are very long. In the latter species each of the processes bears a minute knobbed process (*pu*), which pierces the puparium as the external spiracle (Fig. 46). The surface of the knob of each of these processes is rough and contains a large number of pores. Each of these external spiracles communicates with a very small felt chamber, which has a minute scar on it. The felt chamber in turn communicates with a tracheal trunk to the internal spiracle.

A pair of internal spiracles (*pui*) are present in all the species including *P. scutatus*. They are situated on each side, at the bases of the processes already mentioned. The internal spiracles of all the species except *Sphaerophoria flavicauda* and *Sph. scripta*, have a single circular or oval opening, interrupted by a variable number of marginal projections, and are covered with minute hairs. The internal spiracles lead directly into the main tracheal trunks without the intervention of a felt chamber. The tracheal trunks enter the developing imago at the point of the future prothoracic spiracles.

Although Metcalf (1913) dealt with the life history and morphology of a large number of aphidophagous Syrphidae, he says: "...in this type there is no evidence whatever of the development of special spiracles for the pupal stage." The present author is of the opinion that a reinvestigation may show the presence of internal spiracles in all syrphid pupae.

INTERNAL ANATOMY

The internal anatomy of the third stage larva of all the species is essentially the same. The few minor differences consist in the size and shape of the various organs. Hence the following account, which is mainly a description of the third stage larva of *Platychirus scutatus*, will apply to the other species.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Figs. 48–53.

Integument

The integument (Fig. 54) of the larva consists of a chitinous cuticle and a single layer of hypodermal cells (*h*), limited internally by a very thin basement membrane. In section the cuticle is seen to have two distinct parts: an outer thin structureless layer known as the epidermis (*ep*), which forms the scales (spinules of other species) and the bases of sensory hairs: and an inner layer, the dermis (*dr*), which is thick and composed of a number of thin lamellae. Both layers are unpigmented and are very flexible. The cuticle of which the anterior and posterior spiracles are formed is hard and the epidermis is brown in colour. It is thinner on the ventral than on the dorsal surface of the larva, and is also thin on the pseudocephalon. The hypodermal cells are flattened and polygonal in shape, as can be seen by cutting a portion of the skin and laying it flat with its inner surface exposed. In sections the partitions between the cells are not visible. Each cell possesses a clear cytoplasm and an ovoid nucleus. The nuclear membrane is distinct and encloses a large number of chromatin granules of varying sizes among which is present a nucleolus. In the region of the third thoracic and first abdominal segments there is a distinct break in the cuticle (Figs. 54 *b* and 55 *b*) along which two plates (Fig. 31, pl^1 and pl^2) will separate at the time of hatching of the puparium.

Fat-body

The fat-body occupies a great part of the body cavity. The masses of fat cells which lie in the dorsal part of the body cavity are opaque and either white or pink, while those which are free in the body fluid, and lie along loops of the alimentary canal and salivary glands, are transparent. Sometimes fat cells in a group are very closely applied to each other, and adjacent groups are connected by fine strands. Fat cells are mostly polygonal in shape, and contain a number of fat globules in addition to a nucleus. Although no crystalline deposits can be seen in the fat cells, opaque cells when immersed in a solution of weak acid produce a slight effervescence, though transparent cells produce no effervescence. This effervescence is probably due to the presence of calcium carbonate in these cells. Calcium is present in comparatively large amounts on the inner surface of the puparium, and it is suggested that its source is the fat-body. An abnormal condition of the fat-body was found in one larva, the

Legends to Figs. 48–53.

Fig. 48. Dorsal view of head and thorax of the pupa of *Platychirus scutatus*. × 9.

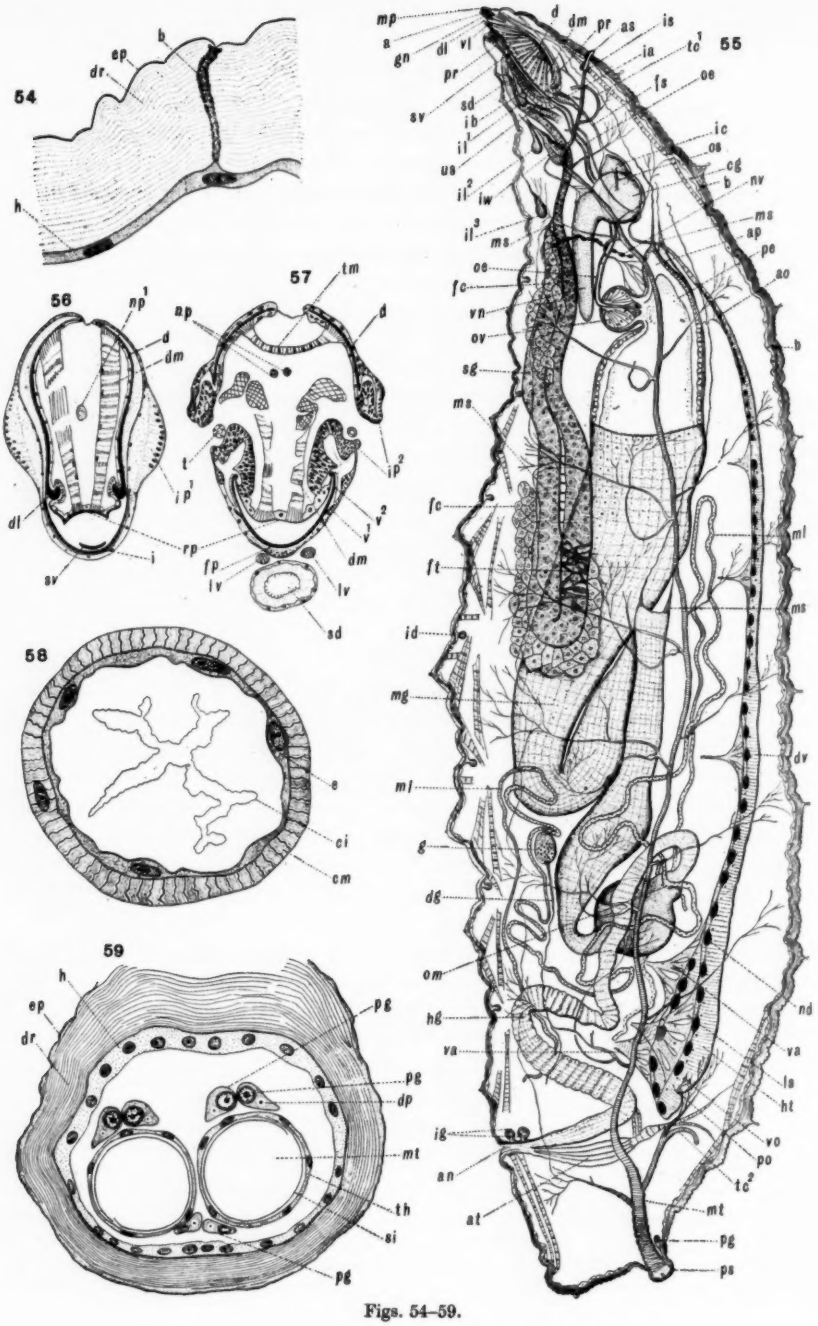
Fig. 49. The thoracic process of the right side with external and internal spiracles of the pupa of *Platychirus scutatus*. × 76.

Fig. 50. Dorsal view of the head and thorax of the pupa of *Syrphus balteatus*. × 12.

Fig. 51. The blind thoracic process of the left side pushed a little to the right to give a full view of the internal spiracle of the pupa of *Syrphus balteatus*. × 118.

Fig. 52. Dorsal view of the thorax of *Sphaerophoria flavicauda*. × 12.

Fig. 53. The blind thoracic process of the right side pushed towards the left to expose the internal spiracle of the pupa of *Sphaerophoria flavicauda*. × 131.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Figs. 54–59.

fat-body containing a number of highly refractile bodies with concentric layers. These bodies, known as calcospherites (Figs. 67–70), have been well described by Keilin (1921) from larvae of *Phytomyzinae* and *Agromyzinae*, and are similar in appearance to starch granules. Keilin is of the opinion that calcospherites, when present, can be found in every individual larva of the species throughout its life. I am inclined to agree with him and consider this isolated case pathological. In the fat body containing calcospherites, the outlines of the fat cells are obliterated. Each calcospherite is formed by a fat cell, which is represented by the outer wall of the former. Sometimes a degenerated nucleus is present (Fig. 68). When examined by polarized light a black cross is seen (Fig. 70), as has been described by Keilin.

Oenocytes

Oenocytes are present in the body of the larva. They are small oval or pear-shaped cells with round nuclei and clear cytoplasm. They are smaller in size than fat cells and are sometimes joined to one another by fine fibrous strands, forming groups or chains. I was not able to find any definite arrangement of the oenocytes in these species of syrphid larvae; some of them are connected with the cells of the fat-body and some lie free in the body cavity.

Muscular attachments

According to Henneguy (1906), Perez (1910) and Keilin (1917), the muscles of insects are attached indirectly to the cuticle, the muscle fibres being connected to the cuticle by certain fibrils. These fibrils are called tonofibrillae,and are said to be secreted by the hypodermal cells and are shed with the cuticle at each moult. Similar structures (Fig. 60, *tf*) have been seen in the larvae of *Platycherus scutatus*, and consist of radiating bands of fibrils, which travel from the muscle terminations, through the hypodermis to varying depths in the cuticle. These tonofibrillae are devoid of striations, and have the same staining reactions as the cuticle.

Pharynx (Figs. 55, 55 A, 56 and 57)

The structure of the pharyngeal skeleton has been already described. The dilator muscles (*dm*) of the pharnyx arise from the inner surface of the dorsal wings (*d*) of the basal plate and radiate to the roof of the pharynx (*rp*), on the

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Legends to Figs. 54–59.

Platychirus scutatus (third stage larva)

Fig. 54. Longitudinal section of the integument of first abdominal segment showing cleavage of the cuticle. × 659.

Fig. 55. Lateral view of the complete larva showing internal anatomy. Oesophageal valve and a part of the mid-gut are shown in longitudinal section. × 23.

Fig. 56. Transverse section of the pharyngeal mass in front of the opening of salivary duct. × 70.

Fig. 57. Transverse section of the posterior half of the pharyngeal mass. × 83.

Fig. 58. Transverse section of the oesophagus. × 536.

Fig. 59. Transverse section at the base of the spiracular projection of posterior spiracles of *Syrphus ribesii* showing perispiracular glands. × 163.

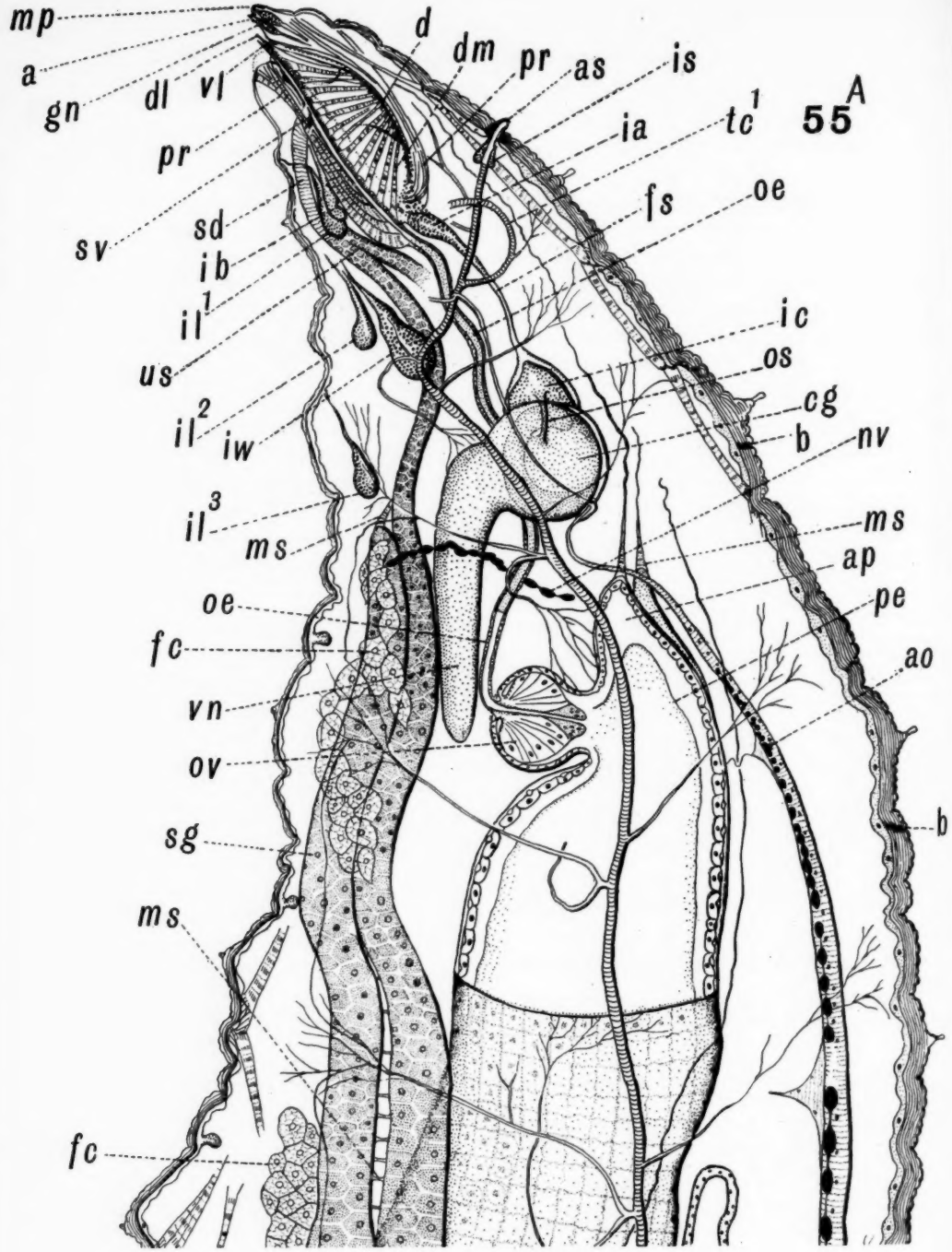


Fig. 55A. Anterior part of Fig. 55 further enlarged. ×58.

dorsal surface of which they are inserted. A number of muscles arise from the inner surface of the anterior part of the pseudocephalon, travel over the outer surface of the dorsal and ventral wings of the basal plate and are inserted on the posterior parts of this plate. They are the protractor muscles (*pr*) of the pharynx and their action during feeding causes the whole pharyngeal mass to move backwards and forwards. The chitinous wings of the basal plates are covered by a layer of hypodermal cells. A curious thickening (ip^1) of this layer is seen on each side of the skeleton in the region where the dorsal wings arise from the basal plate, and consists of two layers of cells, the nuclei of the inner lying close to the chitinous skeleton, and those of the outer layer lying near the periphery. In a transverse section the cell boundaries cannot be seen. The cytoplasm of the outer layer shows faint wavy transverse lines. The thickening is continued backwards (ip^2) for a short distance over the edges of the dorsal and ventral wings of the basal plate. This thickening is the pharyngeal imaginal bud.

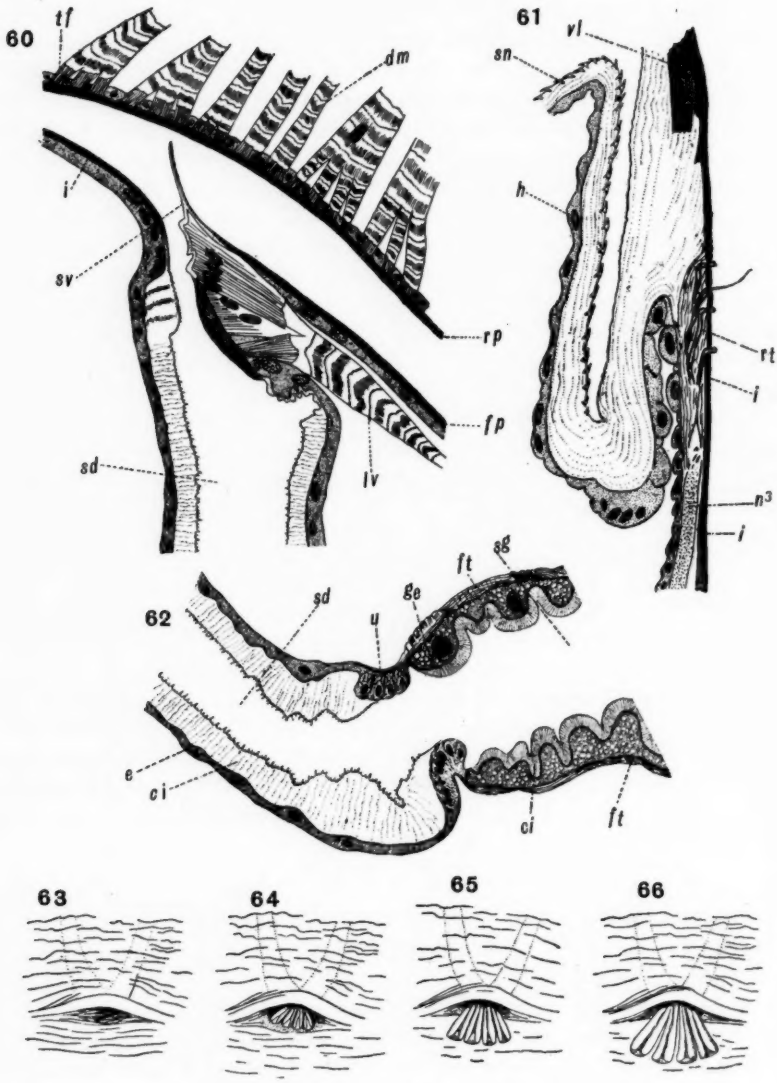
The floor of the pharnyx is devoid of longitudinal ridges, and this is in accordance with the carnivorous mode of life of the larva, for Keilin (1915) has shown that the absence of these ridges is characteristic for all cyclorrhaphous larvae feeding on living tissues.

Oesophagus (Figs. 55, 58 and 55A)

The pharynx is continued posteriorly as a narrow tube—the oesophagus (*oe*). The wall of the oesophagus consists of an outer layer of circular muscle (*cm*) and an inner layer of epithelial cells (*e*). A chitinous intima (*ci*), which is a backward prolongation of the pharyngeal skeleton lies as a free tube in the lumen of the oesophagus. The oesophagus passes between the cerebral hemispheres and the ventral nerve mass, and ends in the oesophageal valve (*ov*). This structure is formed by the excessive growth and elongation of a group of cells, which results in a pear-shaped valve. The valve is situated in the third thoracic segment.

Mid-gut (Figs. 55 and 55 A)

The oesophageal valve opens into the mid-gut (*mg*) on the ventral side of the anterior part of the latter. At its commencement the mid-gut is wide and has two pouches (*ap*), which arise from the dorsal surface of its anterior end. The two pouches are connected by muscle fibres (*ms*) to the pseudo-cephalon. The mid-gut narrows posteriorly and at about the fifth abdominal segment forms a loop which travels forwards to form another loop in about the third or fourth thoracic segment. Two muscle bands connect this second loop of the mid-gut to the pseudocephalon. It then continues posteriorly to about the sixth abdominal segment, where it enters the hind-gut. The terminal part of the mid-gut is dilated, and into the hinder part of the dilatation open the four malpighian tubules. The wall of the mid-gut consists of an outermost layer of longitudinal muscles, a middle layer of circular muscles and an innermost layer



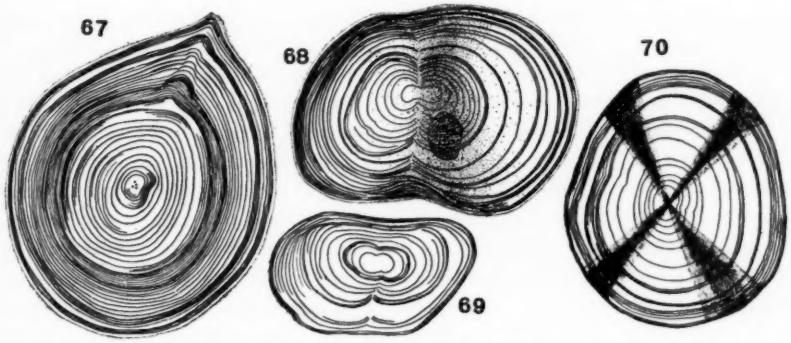
Platychirus scutatus (third stage larva)

Fig. 60. Valve at the opening of salivary duct into the pharynx. ×380.
Fig. 61. Longitudinal section of the hypopharyngeal sense organ. ×475.
Fig. 62. Longitudinal section of a part of the salivary gland where it opens into the common salivary duct. ×325.
Figs. 63–66. Anus showing evagination of anal tubes. ×31.

of epithelial cells. The cytoplasm of the epithelial cells is vacuolated. A thin petritrophic membrane (*pe*) lines the mid-gut.

Hind-gut (Fig. 55)

The hind-gut extends from the sixth to the eighth abdominal segment. It becomes wider as it travels posteriorly, and forms a wide loop directed ventrally in the seventh abdominal segment. Its wall consists of an outermost layer of longitudinal muscles, a middle layer of annular muscles, and an innermost layer of epithelial cells. The layer of annular muscles is well developed in the hind-gut, and a chitinous intima is present lining the lumen.



Figs. 67–70. Calcospherites from the fat-body of *Platychirus scutatus*. One of them shown with a black cross which appears on examination under polarized light. ×200.

Anus (Fig. 55)

The hind-gut opens into the anus (*an*) in the eighth abdominal segment by means of a short canal, which consists of an outer layer of hypodermal cells and an inner layer of chitin. Its posterior surface is connected to the posterior end of the body by means of two bands of muscles. Four anal tubes (*at*) open into the anus at its commencement. They are formed of epithelial cells lined by a thin chitinous membrane. A group of muscles is present at the free ends of the anal tubes. Two of these muscles join these tubes to the hind-gut, and the remaining fibres radiate towards the dorsal surface of the body wall. The anal tubes are usually retained within the body of the larva, but when a larva is deprived of food and left on a wet surface the anal tubes may be evaginated through the anus (Figs. 63–66).

Salivary glands (Figs. 55, 60, 62 and 55 A)

The salivary glands (*sg*) are well developed structures, one lying on either side in the anterior half of the body, ventral to the mid-gut. Each gland is tubular and extends backwards to the fourth abdominal segment, where it forms a loop and travels forwards to its termination in the first thoracic seg-

ment. The termination is blind and is connected to the anterior narrow part of the gland by a band of muscle. The loop is the widest part of the gland, and is embedded in fat cells (*fc*). The two limbs of the loop are held together by transverse bands of striated muscle (*ms*). The anterior narrow end of the salivary glands of each side unite below the posterior end of the pharyngeal mass, to form the common salivary duct (*sd*), which opens by means of a wide aperture situated in the hypopharynx. This aperture is guarded by a tongue-like chitinous valve (*sv*), to the base of which are attached a pair of strong muscles, which are inserted on the ventral surface of the basal wing. The wall of the gland is made up of a single layer of large epithelial cells projecting into the lumen, and a chitinous intimal layer lining these cells. The cytoplasm of these cells has numerous small vacuoles. The chitinous intima shows fine striations.

There is a bundle of intersecting muscle-fibres (Fig. 62, *ft*) surrounding the outer surface of each salivary gland. This network has been called the "fibrillary tunic" by Keilin (1917) who believed it to be formed of a special kind of striated muscle, wherein the striations differed from those of ordinary striated muscle. In the opinion of the present writer it is unnecessary to make this distinction, for under suitable conditions the striations may be seen clearly. For this purpose the larva is killed quickly by immersion in hot water, this precaution being necessary in order to obtain the salivary gland in an inactive stage. The gland may then be dissected out and the coagulated saliva extracted and wall of the gland spread out on a slide. Under the microscope all the bundles will then be seen to have the usual striations found in the muscle of insects. Without some such treatment the striations are liable to be obscured, either by the staining of the epithelium in course of preparation, or by the wrinkling of the fibres in contraction.

The division (*u*) between the common duct and each gland is marked by a group of small cells, whose outlines are easily seen, and which causes a constriction of the lumen at this point. The chitinous intima is very thin over these cells. The wall of the duct consists of flattened epithelial cells and a chitinous intima, which is thick and has fine ridges on its internal surface. The wall of the duct has no "fibrillar tunic".

Malpighian tubes

Four malpighian tubes (Fig. 55, *ml*), two on either side, are present in the body cavity. One of each of these is situated dorsally and the other ventrally. The dorsal tube is the longer and reaches to the second or even the first abdominal segment. The ventral tube is shorter and has many convolutions in the posterior half of the larva. Both tubes end in the seventh abdominal segment. The two tubes of each side open close together (*om*) in the dilated part of the mid-gut. In transverse section each tube consists of two cells which bulge into the lumen and have well marked nuclei. Sometimes yellow granules

are seen in the cytoplasm of the cells. They are probably of an excretory nature. The inner margin of the cell is finely striated.

Tracheal system (Figs. 55 and 55 A)

There are two main longitudinal tracheal trunks (*mt*) extending between the prothoracic and posterior spiracles. They lie one on either side of the body cavity of the larva, and are connected by eleven dorsal commissures (one in each body segment), the first (tc^1) and the last (tc^2) commissures being very prominent. The first commissure lies in the first thoracic segment, and gives off a pair of branches which run forwards over the pharyngeal mass into the pseudocephalon. The last and thickest commissure lies in the eighth abdominal segment, where it forms an anterior loop and gives off a pair of tracheal tubes from its anterior part. These tubes ramify profusely over the posterior dilated part of the dorsal blood vessel (heart) (*ht*). The other commissures are very slender and form inverted V-shaped loops, from which arise a number of finer branches to supply the dorsal body wall. Eleven tracheal tubes arise from the ventro-lateral side of each main trunk; each divides into two, a short distance from its point of origin, one branch travelling to the ventral body wall and the other turning inwards to supply the viscera. The branch supplying the ventral body wall gives off a small branch, which supplies the lateral body wall, and further divides into fine tracheoles. From the first to the seventh abdominal segment, each of these tracheoles is connected to a tracheole of an adjacent branch by means of a fine longitudinal commissure. Thus seven longitudinal commissures are formed intersegmentally on each side of the ventral part of the body constituting a rudimentary tracheal trunk.

The main tracheal trunks and the larger vessels consist of closely applied polygonal cells, internal to which is a chitinous intima with thick spiral taenidia (Fig. 72, *mt*). The terminal branches of the tracheoles do not show the spiral taenidia.

The anterior and posterior spiracles have been already described. The felt chamber of the prothoracic spiracle and the terminal part of the main tracheal trunk is surrounded by a pear-shaped structure, which is the imaginal disk of the pupal prothoracic spiracle (Fig. 55 A, *is*). The perispiracular glands of the anterior spiracle have not been seen by the writer but they were described by Krüger (1926) in *Syritta pipiens*. The perispiracular glands of the post-abdominal spiracles are eight in number—four being present on each side. Fig. 59 shows three of these glands (*pg*) on each side, the fourth, being situated deeper, is not seen. Each gland consists of a single cell with a large round nucleus and a prominent nucleolus. Intracellular ducts (*dp*) lead from each cell to the opening of the corresponding gland, one of the ducts dividing at its terminal part to supply the double opening. The function of secreting a waxy or oily material, which prevents wetting of the spiracular plates, has been assigned to these glands by previous authors.

Nervous system (Figs. 55, 72 and 55 A)

As in all cyclorrhaphous Diptera the central nervous system of the larva is characterized by the condensation of the ventral ganglia into a single ventral nerve mass (*vn*), called the neuroblast by Lowne. The brain consists of two cerebral lobes of ganglia (*cg*), which are connected by means of a very small supraoesophageal commissure. At the sides the cerebral lobes embrace the oseophagus and become fused with the anterior broad end of the ventral nerve mass. Except for the paired nerves arising from it, the ventral nerve mass does not show any superficial evidence of its composite origin. The brain, together with the ventral nerve mass, occupies the whole length of the first abdominal segment. Its position varies sometimes, because it is connected by cephalic buds to the pharyngeal mass and movements of the pharyngeal mass affect its position. The ventral nerve mass sends out several pairs of nerves and receives numerous tracheae. Each of the abdominal nerves is closely associated with a trachea, which enters the nerve mass close to the root of the nerve. Most of the nerves that arise from the ventral nerve mass have been followed to their terminations. The following is a list of these nerves:

(1) A pair of nerves (*nr*) arise from the points of the union of the cerebral ganglia with the ventral nerve mass and travel forwards. On reaching the pharyngeal mass each of them gives off a lateral branch and continues forwards to end in the nerve ganglion of the antenna. The lateral branch anastomoses with a branch of a nerve belonging to the set of bifurcated nerves described below.

(2) A pair of nerves (n^1) from the anterior border of the ventral nerve mass travels forwards, passes through the protractor muscles of the pharynx, gives a branch to the buccal-sense organ and ends in the ganglion of the maxilla.

(3) Two pairs of nerves (n^2) arise from the anterior border of the ventral nerve mass, run in straight lines along the oesophagus and end in the protractor muscles of the pharynx.

(4) A pair of nerves (n^3) travel on the ventral surface of the pharyngeal mass, and penetrate the latter at its anterior part. They are probably the nerves which supply the sense organs of the hypopharynx (Fig. 61).

(5) A pair of nerves (n^4) supply the labial imaginal disks.

(6) Four pairs of thoracic nerves: three of these (n^5) supply the imaginal disks of the legs and the body wall of the corresponding segments and the fourth (n^6) supplies the imaginal disks of the wings.

(7) Eight pairs of abdominal nerves (n^7)—one pair supplying each abdominal segment.

(8) Six nerves (n^8) arise in the medio-dorsal line of the ventral nerve mass. Hewitt (1914) recognized three such nerves in the larva of the domestic fly, and called them accessory nerves. Keilin (1917) saw three similarly situated nerves in the larva of *Phoania cincta*, and termed them bifurcated nerves. The writer has seen six of these nerves, two of which bifurcate very near their

origin, while the other four bifurcate at increasing distances. The first nerve after bifurcating forms a plexus mainly in the first thoracic segment and the pseudocephalon. The second nerve forms plexuses in the second and third thoracic segments. The remaining four nerves mainly supply the muscles of the ventral body wall, and send branches to the points where the chords of the alary muscle are inserted, as shown in Fig. 72.

Sympathetic nervous system (Figs. 72 and 74)

The anterior end of the dorsal vessel (*dv*[1]) is encircled by a structure known as Weismann's ring (*wr*), which is attached by fibrous strands to the outer sheath of the central nervous system. It is penetrated by tracheoles. On its ventral surface is attached a nerve ganglion—Burtt's median ganglion—(*gd*), from which arises a stomatogastric nerve (*sm*). This nerve gives off the recurrent nerve (*rn*), and continues backwards to the dorsal surface of the oesophagus, where it bifurcates. At a little distance from the bifurcation each branch forms a small ganglion and continuing reunites with its fellow to form a nerve-ring round the proventriculus. At intervals around this ring further minor branches are given off, forming a plexus of small nerves which also surrounds the proventriculus. The recurrent nerve runs forwards sending off a small branch which forms a small ganglion (*go*) on the oesophagus, and ends in the frontal ganglion (*gf*), which is situated on the dorsal side of the pharynx deep to the pharyngeal muscles. Two nerves (*np*) arise from the anterior side of the frontal ganglion, unite (*np*[1]) and enter the space between the dilator muscles of the pharynx. Another nerve (*nc*) arises from either side of the ganglion, runs backwards and joins the central nervous system at the point of fusion of the cerebral lobes with the ventral nerve mass.

Weismann's ring was discovered by Weismann (1864) in *Calliphora*. He believed it and the stomatogastric nerve to be muscular supporting structures for the dorsal vessel. Künckel d'Herculais (1875) found it in the larva of *Volucella* (Syrphidae), Lowne (1890–95) in *Calliphora* and Pantel (1898) in the larva of *Thrixion*. Hewitt (1914) describes it in *Musca domestica* and Keilin (1917) in the carnivorous Anthomyid larva *Phaonia cincta*. The true function of this ring was not known till Burtt (1937) showed that it represents the fused corpora allata of other insects. Wigglesworth (1934) had already found in the reduviid bug *Rhodnius prolixus* that these corpora allata have the function of secreting a hormone which induces moulting and metamorphosis. Fraenkel (1935) too, working on *Calliphora erythrocephala*, found a hormone which induced pupation and which was produced in the region of the central nervous system. He was not able to discover what organ produced the hormone.

Sense organs (Figs. 61, 71 and 73)

On examining the sections of most of the sense organs (except the antennomaxillary complex and the buccal sense organ), one finds that they consist of refractile tubes. The number of these tubes in a particular organ varies

according to the number of sensory spots or knobs present on the exposed terminal part of the organ. A sensory papilla from the dorsal surface of the head (Fig. 73), and another from the ventral surface of the first thoracic segment (Fig. 71) are described below.

Each sensory papilla on the dorsal surface of the pseudocephalon is conical in shape, with a cup-shaped depression (*c*) at its apex. From the centre of the bottom of the cup arises a minute knob-like structure, around the base of which is a ring of thickened chitin. From this ring a refractile tube (*rt*) leads inwards, traverses the whole thickness of the cuticle and is connected to the nerve centre (*gs*). The wall of the tube stains deeply with haemalum and other stains and is generally thickened in two places, one near its middle and the other near its inner termination. An axial filament (*ax*) runs inside the tube.

Each ventral sensory papilla (Fig. 71) is very similar to the dorsal papilla described above, except that it is smaller and nipple-like and the nerve centre that supplies the base of the tube has a longer and finer nerve.

The sensory hairs of the abdominal segments have two parts, a basal and a distal. The basal part has a pit on one side, containing two sensory refractile spots, from which two tubes go to the adjacent nerve-centre.

The antenno-maxillary palps have fine fibres leading from the sensory spots into their respective nerve centres (ganglia).

Two sense-organs of a special kind are present on the floor of the hypopharynx (Figs. 44, *hs* and 61). They appear as oval areas, each containing a group of minute rounded projections and a fine hair. From these sense organ tubes proceed backward and inward and enter the nerve supply of the sense organ. The wall of the tube is thickened in two or three places. An axial filament is present within each tube. This organ was first described by Keilin for syrphid larvae in his unpublished records, to which he has kindly given me access. Similar refractile tubes were also found by Keilin (1911) in the larva of *Phora*. He showed them to be chitinous structures which are shed with each larval moult.

Imaginal disks (Figs. 55, 72 and 55 A)

Cephalic disks. The main cephalic disks develop within a hypodermal involution, called by Snodgrass (1924) the frontal sac. It appears on the dorsal surface of the posterior end of the pharyngeal skeleton, and, after forming a pair of thickenings (the antennary disks) is continued backwards as a narrow band made up of two fine cellular membranes, closely opposed. This sac ends posteriorly in a pair of lateral sac-like expansions, which rest on the anterior surface of the cerebral ganglia. Within each expansion is the conical imaginal disk of the compound eye (*ic*). Each of these disks is connected laterally with the corresponding cerebral ganglion by means of an optic stalk (*os*). On the lateral surface of each cerebral ganglion, and enclosed in its sheath, is a semicircular thickening. This thickening is comparable to the retinal imaginal disk seen by Lowne in the larva of the blow-fly. The pharyngeal

imaginal disks (Figs. 50 and 51, ip^1 and ip^2) have been already described. Labial imaginal disks (*ib*) are present on the ventral surface of the pharyngeal mass. They are pear-shaped and connected anteriorly by means of fine stalks to the hypopharynx anterior to the opening of the salivary duct. The maxillary imaginal disks are also pear-shaped, situated ventro-lateral to the pharyngeal mass. Their fine anterior thread-like stalks travel on the ventral surface of the pharyngeal mass and end in the lateral wall of the mouth of the larva. Künckel d'Herculais illustrated a pair of mandibular disks in the larva of Volucella. They were not found in any of the species described in this paper.

Thoracic disks

There are five pairs of thoracic buds, four pairs being present in the ventro-lateral part of the body cavity. Three pairs of buds, the limb buds (il^1, il^2 and il^3), are attached by fine stalks to the ventral body wall of the first and second and third thoracic segments respectively. The fourth and largest, the wing bud (*iw*), is attached to the second thoracic segment by a fine stalk. Imaginal disks are well supplied with tracheoles and have an independent nerve supply. The present author was unable to see the groups of fine sensory hairs described by Keilin (1915), as being present on the surface in all dipterous larvae marking the point of attachment of the stalks of the thoracic buds to the body wall. The fifth pair of thoracic imaginal disks, that of the pupal prothoracic spiracles (Fig. 55 A, *is*) surrounds the felt chamber of the prothoracic spiracles.

Abdominal disks

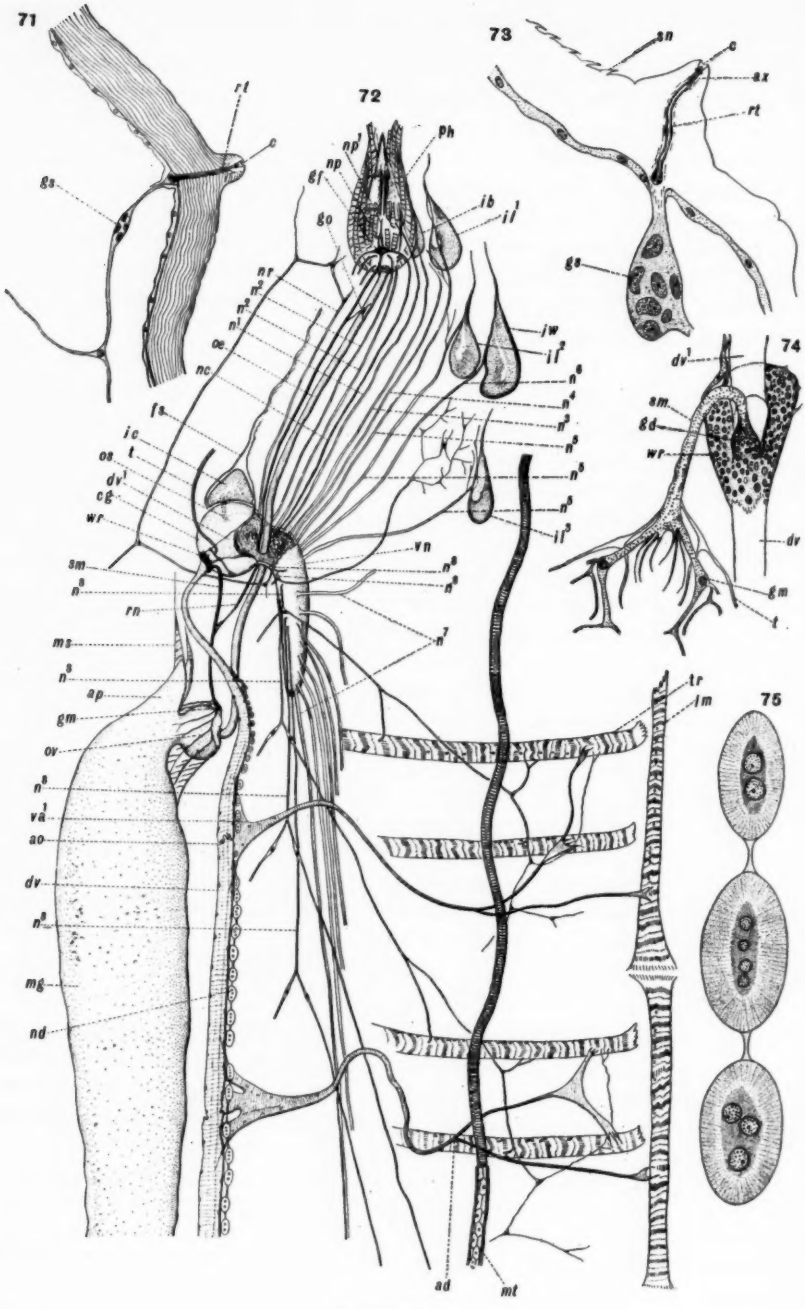
Seven pairs of abdominal imaginal disks (*id*) are found within the cuticle as tubercles on the ventral body wall, one pair being present in each of the first seven segments. Ganin (1876) in his work on muscid larvae describes similar paired abdominal thickenings, which he thought give rise to the musculature of the abdominal segments of the imago. In the eighth segment two pairs of buds are seen attached to the anterior wall of the anal canal. These ultimately form the genitalia.

Gonads (Fig. 55)

The gonads (*g*) are represented by a pair of oval bodies, embedded in a mass of fat cells, and situated in the ventral part of the posterior half of the body cavity. They consist of numerous cells of varying sizes enclosed in a membrane. From the posterior end of each gonad a long filamentous duct (*dg*) arises and travels towards the imaginal disks of the genitalia.

Circulatory system (Figs. 55 and 72)

The dorsal blood vessel (*dv*) is a straight muscular tube which runs mediodorsally from the third thoracic to the seventh abdominal segment. It lies immediately below the dorsal body wall, and is narrow anteriorly and wide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Figs. 71–75.

posteriorly. The anterior narrow end of the vessel turns towards the central nervous system, passes through the Weismann's ring and enters the space between the cerebral ganglia. Here it ends in a thin-walled funnel-shaped structure (Fig. 72, *dv*[1]), the edges of whose opening are fused with the envelope of the central nervous system and the membrane of the frontal sac. Two tracheoles arising from the main tracheal trunk lie in close relation to the funnel-shaped structure. They have an intercommunicating branch which lies on the dorsal surface of the funnel, and two branches which supply Weismann's ring.

Two pairs of ostia (*ao*, *po*) are present in the wall of the dorsal vessel, each opening being guarded by a valve (*vo*). The valve is formed by two cells with prominent nuclei and filamentous ends. The first pair of ostia (*ao*) is situated in the second abdominal segment at the origin of the first pair of alary muscles, the second posteriorly (*po*), close to the end of the heart, usually in the 7th abdominal segment. The posterior dilated portion of the vessel forms the heart proper (*ht*), a constriction close to the posterior ostia dividing its cavity into two chambers. The dorsal surface of the heart is richly supplied with tracheoles from the last tracheal commissure. Constrictions of the dorsal vessel are also present at the origins of the second, third and fourth alary muscles, but no ostia have been seen.

The four pairs of anterior muscles (Fig. 72) have their origin along a pair of longitudinal lines on the ventral surface of the dorsal blood vessel, and narrow as they travel laterally. When the narrow cord-like part reaches the main tracheal trunk it divides into two branches, one going ventral to the trunk, to be inserted in the transverse muscle of the ventral body wall, and the other dorsal to the trunk, to be attached to the longitudinal muscle of the body wall. Before insertion each of these branches expands into a delicate web and is ultimately attached to the muscles of the body wall by means of short fibrils.

Three further pairs of alary muscles (Fig. 55) take their origin from the wall of the heart; two pairs (*va*) from its ventral part, and one pair (*la*) from its dorsal part.

Nephrocytes (Figs. 55, 72 and 75)

Nephrocytes of all cyclorrhaphous Diptera may be classified as (*a*) pericardial or dorsal (*nd*) and (*b*) perioesophageal or ventral (*nv*). Their presence can be demonstrated in a living larva by an injection of ammonia-carmine into the body cavity (Keilin, 1917). This injection, in addition to demonstrating

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Legends to Figs. 71–75.

Platychirus scutatus (third stage larva)

Fig. 71. A sensory papilla from the ventral surface of first thoracic segment. ×318.

Fig. 72. Nervous system and the anterior part of dorsal blood vessel with its alary muscles. Sympathetic nervous system is shown in darker line. ×32.

Fig. 73. A sensory papilla from the dorsal surface of pseudocephalon. ×1000.

Fig. 74. Ventral view of Weismann's ring and the stomatogastric nerve. ×111.

Fig. 75. Pericardial nephrocytes. ×240.

the presence of nephrocytes, shows their function of removing useless material from the blood.

(*a*) The dorsal group consists of a row of nephrocytes situated on either side of the dorsal blood vessel. The anterior nephrocytes, e.g. in the first abdominal segment, are small round cells with a single nucleus. They overlap one another and may be present in groups. The other nephrocytes (Fig. 75) are large oval cells having two to four nuclei, and sometimes connected together by fine strands. Round the heart there are two rows of nephrocytes, dorso-lateral and ventro-lateral on either side. The cytoplasm of the large nephrocytes is striated peripherally and granular in the middle (Fig. 75).

(*b*) The ventral group forms a chain which runs beneath the oesophagus from the fat cells at the anterior end of one salivary gland to those of the other. Each of these nephrocytes is a small cell with two nuclei. Some of them lie close together, the more distant being connected together by fine strands.

Discussion

Apart from Keilin, few authors have studied the morphology of the early stages of syrphid larvae; in fact even the existence of these early stages has been doubted.

Vine (1894) believed that the larvae reach maturity simply by a process of growth, and with regard to the moulting of the cuticle says: "I have satisfied myself, after a long series of observations that nothing of the kind occurs in aphidophagous Syrphidae."

Metcalf (1913), without knowing the number of moults shed by the larva before reaching maturity, said that moulting probably did occur but consisted of a "somewhat continuous process of shedding flake-like pieces".

In this paper it has been shown that these larvae pass through three stages, separated by two moults as is the case in most cyclorrhaphous larvae. The process of moulting is preceded by extrusion of the faeces, this process only occurring at ecdysis. The reason why moulted skins have not been seen by many workers is that these skins are very thin and transparent and remain adherent to the surface on which they are shed. If however the skin is shed on a clean glass dish it can be easily seen.

The buccopharyngeal armature of all the aphidophagous syrphid larvae is remarkable for the uniformity of its structure. In the first stage the dorsal and ventral lips are thin and blade-like, and the ventral lip has a saucer-like projection at its base. There is no outer wing of the basal plate, and the roof of the pharynx shows no strongly chitinized band. One pair of lateral rods (lt^1) is present, not connected with the skeleton. In the second stage the dorsal and ventral lips are strongly chitinized inverted V-shaped structures, and the latter has no saucer-like projection. A pair of comb-like sclerites (*cs*) has appeared at the sides of the mouth. A second pair of lateral rods (lt^2) has developed from the skeleton at the angle formed by the two lips. An outer

wing (*v'*) of the basal plate is present. The roof of the pharynx has a longitudinal chitinized band (*rp*) in some species. In the third stage the cephalopharyngeal armature is even more chitinized, and a pair of triangular sclerites (*ts*) and the third pair of lateral rods (lt^3) are formed.

Metcalf (1913) called the mouth parts "mouth hooklets" and found that they varied in number. The present writer finds the only variation in the mouth-parts of these species is one of degree of chitinization and relative size of the various parts.

The presence of both upper and lower lips in the larvae of Syrphidae is a character of importance. As shown by Keilin (1915) the Aschiza, to which the Syrphinae belong, form a group whose members are linked by the similarity of their buccopharyngeal armature. This may be roughly described as reduction of the intermediate sclerite and a great development of the dorsal and ventral lips.

Keilin has shown that the upper lip is common to all first stage larvae belonging to the cyclorrhaphous Diptera. He points out that in the Aschiza it persists through all the three larval stages, and is more and more chitinized from the first to the third stage in Syrphinae, though it tends to lose its chitinization through the three stages in Phoridae, Platypezidae, Lonchopteridae, Pipunculidae and Conopidae. The syrphid larvae examined by the writer have confirmed Keilin's view, both upper and lower lips being present in the three larval stages and becoming more and more chitinized in the two last stages.

The upper and lower lips of syrphid larvae described in this paper are sharply pointed and are adapted for piercing. This character is connected with their carnivorous mode of life, as are the other characters indicated below.

The salivary gland has many features only known in carnivorous larvae. Its outer surface is surrounded by a network of fibrillar tissue, the "fibrillar tunic" of Keilin (1917), which he found only in carnivorous anthomyid and syrphid larvae. The very wide salivary duct is common to all carnivorous forms. Syrphid larvae secrete a large amount of rather sticky saliva, which is used for movement on a smooth surface, for attachment before pupation, but also for entangling their prey.

The floor of the pharynx is devoid of ridges. This character has been shown by Keilin (1915) to be typical of all the biontophagous larvae feeding upon living material (carnivorous, phytophagous and parasitic).

The mid-gut is short and this again suggests that these larvae have carnivorous habits, for saprophytic larvae tend to have much longer intestines.

The characters cited above and the direct observation of feeding habits, leave no doubt as to the carnivorous mode of life of these larvae. Some observers such as Verrall (1901) in the cases of *Platychirus scutatus* and *Sphaerophoria flavicauda* have been misled about their feeding habits through finding larvae or pupae in atypical situations. The reason for their being found in such situations is that the pupae of most of the species are formed on dry

leaves, and these leaves falling to the ground may be carried to a quite unwonted situation. Thus Krüger (1926) found a larva of *Platychirus scutatus* while sweeping in a pond with a plankton net.

The changes which take place in the respiratory system through the three stages are very characteristic. The first stage larva is metapneustic, only one pair of spiracles being present, situated wide apart on the eighth abdominal segment. Each spiracle has two openings, the partition between the openings being incomplete. A single opening of the perispiracular gland is present on each spiracular plate. In the second stage the larva is amphipneustic, one pair of spiracles with single openings being present on the first thoracic segment and the other on the eighth abdominal segment. The posterior spiracles are still wide apart, and have three spiracular openings. A spiracular scar of the previous stage, and four openings of the perispiracular glands (one of these openings being double) are present. Second stage larvae of other cyclorrhaphous Diptera, as described by Keilin and other workers, have only two openings on each posterior spiracle, e.g. (1915) *Pollenia rudis* (1917) *Muscina assimilis*, and (1919) *Melinda cognata* Meig. In some abnormal cases of second stage larvae of *Melinda cognata* Keilin found three spiracular openings. In all cases the syrphid larvae described in this paper have three openings in the posterior spiracles.

The third stage larva is also amphipneustic. The thoracic spiracles have a spiracular scar and a single opening with an uneven margin. The posterior spiracles are now strongly chitinized and fused together medially. They have three slit-like spiracular openings on each plate, and these openings are raised on projections of which the size varies with the species. A spiracular scar of the preceding stage is present, and four perispiracular glands. In most of the species the openings of these glands lead into short canals on the surface. It is interesting to note that the posterior spiracles which are fused and situated on prominences have much the appearance of a retracted syphon of aquatic dipterous larvae, suggesting the evolution of these carnivorous species from forms (like eristallines) adapted to an aquatic mode of life.

Structures, hitherto undescribed in syrphid larvae, are the four anal tubes, which are probably vestigial structures. Their presence gives another indication of the evolution of these larvae from some aquatic form.

The antenno-maxillary organs are fused and compact and this feature is common to all the syrphid larvae.

Of special interest is the break or gap in the skin of the third stage larva, in the region of the third thoracic and first abdominal segments. This gap marks the position of the line of cleavage in the pupal skin through which the adult will emerge. As already described (p. 82), emergence takes place by means of the separation of the two plates at the anterior end. The researches of De Meijere (1900) and Keilin (1911, 1915, 1917) have already shown that the annular dehiscence of the anterior end of the puparium by means of a circular cap is by no means the only mode of hatching in cyclorrhaphous Dip-

tera. The method of hatching in the species here described is, however, somewhat similar to that described by Keilin (1911) for the genus *Phora*.

It has been shown by the author that no prepupal stage exists. New structures found in the pupae of all these species are a pair of swellings on the dorsum of the thorax and a pair of pseudopods on each of the abdominal segments. A pair of swellings on the head, e.g. the subocular lobes, similar to the one described by Künckel d'Herculais in Volucellinae and Snodgrass in *Rhagoletis pomonella*, are also found. The author has suggested that the swellings and pseudopods of the pupae may be concerned with the moulding of the shape and hatching of the puparia.

A pair of processes arising from the anterior margin of the dorsum of the thorax is a characteristic feature of the pupae of all the species. They are blind and remain inside the puparium in all the species except *Platychirus scutatus*. In the latter they give rise to external pupal spiracles. Internal pupal spiracles are present in all the species at the bases of the processes.

It is interesting to note that the ventral nerve mass grows very little in size from first to third stage (pp. 88 and 95) as compared to the body of the larva. Thompson (1920) made a similar observation in the larvae of *Miltogramma punctatum* Meig.

The six pairs of bifurcated nerves which arise from the ventral nerve mass are of special interest. Hewitt (1914) and Keilin (1917) described three such pairs of nerves in the larvae of the house fly and *Phaonia cincta* respectively. Of the six pairs found in syrphid larvae, the four posterior pairs supply the terminations of the alary muscles.

Among the sense organs the hypopharyngeal sense organs, which are probably gustatory in function, have been noted before only by Keilin.

The terminations of the alary muscles have been carefully traced and found to divide into two cord-like branches, which travel dorsal and ventral to the main tracheal trunk, to be inserted in the body wall. The relation of these cords to the tracheal trunk suggests a possible mechanism which would aid respiration, for contraction and expansion of the alary muscles would affect both the length and the diameter of the tracheal trunk.

SUMMARY

The paper deals with the biology, morphology and anatomy of seven species of syrphid larvae viz. *Syrphus luniger* Meig., *S. balteatus* De Greer, *S. ribesii* Linne, *Catabomba pyrastri* Linne, *Sphaerophoria flavicauda* Zett., *Sph. scripta* Linne, and *Platychirus scutatus* Meig.

The habitat, mode of progression, aphidophagous habits and characteristic coloration are described for each species.

It is shown that the larvae of all the above species, like larvae of other cyclorrhaphous Diptera, definitely pass through three stages separated by two moults. The mode of dehiscence of the puparium is described briefly.

Each of the species, except *Catabomba pyrastri*, has three generations in the breeding season which lasts from May to October. *Platychirus scutatus* hibernates only in the larval stage, but the other species may be found in both the larval and pupal stages during the winter.

The larvae of all the above species, except *Syrphus balteatus*, are commonly parasitized by ichneumonid larvae.

The morphology of the egg, the three larval stages and the puparium of *S. luniger* is described in detail.

The characters common to the third stage larvae of all the species dealt with are summarized and short descriptions of the third stage larvae and puparia of the individual species are given. The general appearance of the living larvae and details of the buccopharyngeal armature, spiracles and puparia of each of the species is represented in figures.

In connexion with the pupae a number of new structures are described and it is suggested that some of them are concerned with the formation of the characteristic shape of the puparium and with the dehiscence of the puparium.

Internal pupal spiracles are present in all the species dealt with, but external pupal spiracles are present only in *Platychirus scutatus*.

The anatomy of *P. scutatus* is described and figured, an account being given of all the structures except the musculature of the body wall. Study of the anatomy affords evidence as to the carnivorous mode of life of the larvae and also indicates that the larvae have evolved from aquatic forms.

The comparative morphology of the Syrphinae is discussed with respect to the relationship of the Syrphinae to other Aschiza and to the cyclorrhaphous Diptera.

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Key to lettering of figures

a	anus.	*ax*	axial filament.
ab	first abdominal segment.	*b*	break in the skin of the larva.
ad	division of alary muscle showing the distribution of the two parts.	*c*	depression at the apex of a sense organ.
		cg	cerebral ganglia.
al^1	first alary muscle of the dorsal blood vessel.	*ci*	chitinous intima.
		cm	layer of circular muscle.
al^2	second alary muscle of the dorsal blood vessel.	*cp*	canals leading from the openings *so* of the perispiracular gland.
an	anus.	*cs*	comb-like sclerites.
ao	anterior ostium with its valve.	*ct*	chitinous strands connecting spiracular scar with scar on felt chamber.
ap	anterior pouches of the mid-gut.		
as	anterior spiracle.	*d*	dorsal wing of basal plate.
at	anal tube.	d^1	feebly chitinized part of *d*.

da pseudopod of pupa.
dg duct of gonad.
dl dorsal lip.
dm dilator muscles of the pharynx.
dp duct of the perispiracular gland.
dr dermis.
dv dorsal blood vessel
dv^1 funnel shaped anterior termination of *dv*.
e epithelial layer.
ep epidermis.
f felt chamber.
fc fat cells.
fp floor of pharynx.
fs frontal sac.
ft network of fibrillar tissue.
g gonad.
gd median ganglion.
ge glandular epithelium.
gf frontal ganglion.
gm ganglion formed by the stomatogastric nerve on the oesophageal valve.
gn ganglion supplying antenna and maxillary palps.
go ganglion on oesophagus formed by branch of recurrent nerve.
gs ganglion of sense organ.
h hypodermis.
hd dorsal sensory hairs.
hg hind-gut.
hr hairs on the spiracular plate
hs hypopharyngeal sense organ
ht heart.
hv ventral sensory hairs.
i hypopharyngeal sclerite.
ia imaginal disk of antenna.
ib labial imaginal disk.
ic imaginal disk of compound eye.
id abdominal imaginal disk.
ig imaginal disk of genitalia.
il^1 imaginal disk of first thoracic limb.
il^2 imaginal disk of second thoracic limb.
il^3 imaginal disk of third thoracic limb.
ip anterior part of pharyngeal imaginal disk
ip^1 posterior part of pharyngeal imaginal disk.
is imaginal disk of pupal prothoracic spiracle.
it internal thoracic process of pupa.
iw imaginal disk of wing.
la laterally attached alary muscle.
ll lateral lobes of the pseudocephalon
lm longitudinal muscle of ventral body wall.
lp locomotory projections.
ls labial sensillae.
lt outer lateral rod.
lt^1 lateral rod arising from angle formed by dorsal and ventral lips.
lt^2 and *lt*^{3} fine lateral rods arising from the angle of mouth.
lv longitudinal muscle of the valve of the salivary duct.
mg mid-gut.
ml malpighian tube.
mp maxillary palp.
ms muscular strand.
mt left main tracheal trunk.
n^1 nerve supplying the buccal sense organ and the ganglion of maxilla.
n^2 two nerves to the protractor muscles of the pharynx.
n^3 nerve to the ventral surface of the pharyngeal mass penetrating its anterior part.
n^4 nerve to the labial imaginal disk.
n^5 nerves to the imaginal disks of the legs.
n^6 nerve to the imaginal disk of the wings.
n^7 eight abdominal nerves only first and eighth labelled.
n^8 six bifurcated nerves.
nc nerve connecting frontal ganglion to central nervous system.
nd dorsal nephrocytes.
np nerves arising from frontal ganglion and entering space between dilator muscles.
np^1 *np* united.
nr nerve supplying the ganglion of antenna.
nv ventral nephrocytes.
o opening of the common salivary duct.
oe oesophagus.
om opening of the malpighian tube into the hind-gut.
op opening of the perispiracular gland.
op^1 double opening of the perispiracular gland.
os optic stalk.
ov oesophageal valve.
p pseudocephalon.
pe peritrophic membrane
pg perispiracular gland.
ph pharyngeal mass.
pi prominence of integument of post-abdominal spiracle.
pj chitinous projection near the spiracular scar.
pl^1 upper plate which separates at the time of hatching.
pl^2 lower plate which separates at the time of hatching.
po posterior ostium.
pr protractor muscles of the pharynx.
ps post-abdominal spiracles.
pu external pupal spiracles.
pui internal pupal spiracles.
rn recurrent nerve.

rp roof of pharynx.
rp^1 strongly chitinized part of *rp*.
rt refractile tube of sense organ.
s buccal sense organ.
sc subocular lobe.
sd common salivary duct.
sf scar on felt chamber.
sg salivary gland.
si spiral intima.
sl spiracular plate of post-abdominal spiracles.
sm stomatogastric nerve.
sn spinules of pseudocephalon.
so spiracular opening.
sp prominence with spiracular opening.
sr spiracular scar.
ss spinules with forked ends.
st sensory pit.
sv valve at opening of salivary duct.
sw dorsal thoracic swelling of pupa.
t tracheole.
tc^1 first dorsal tracheal commissure.
tc^2 last dorsal tracheal commissure.
tf tonofibrils.
th tracheal hypodermis.
tk thickened brown area in the roof of mouth.
tm transverse band of muscle connecting dorsal wings of basal plate.
ts triangular sclerite.
tr transverse muscle of ventral body wall.
u union of salivary glands and duct.
us point of union of salivary glands.
v^1 outer wing of basal plate.
v^2 inner wing of basal plate.
va ventrally attached alary muscle.
va^1 alary muscle showing line of attachment on the ventral surface of dorsal vessel.
vl ventral lip.
vn ventral nerve mass.
vo valve of ostium.
vs saucer-like projections at the base of the ventral lip.
wr Weismann's ring.

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A CASE OF HUMAN MYIASIS DUE TO *HYPODERMA*

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Cases of myiasis by *Hypoderma* in a human subject in Great Britain are of sufficient rarity to warrant the recording of the following case.

A larva taken from a "small abscess on the neck of a boy aged 10", was sent to the British Museum (Natural History) by Mr Colin Matheson of the National Museum of Wales, with a request that it be identified. The specimen was not in particularly good condition but after examination it was determined as a fully grown first stage larva of *Hypoderma bovis* de G. (the "second stage" larva of MacDougall (1930), "third stage" of Laake (1921), "first stage" of Knipling (1935)).

On further inquiry the following history of the case was received from Dr Lindsay Isaac of the Royal Infirmary, Cardiff:

November 1936. Oedema of the left leg (provisional diagnosis of lymphatic obstruction). Sent in to our out-patient department, but by then the oedema had gone. Later it appeared and went again.

2 *weeks later*. Swelling on left side of abdomen. Provisional diagnosis of *tabes mesenterica*, which was confirmed by our out-patient surgeon.

Sent later to the T.B. people but the lump had then gone and they said "no evidence of T.B."

3 *weeks later still*. Swelling (non-glandular) appeared in the left supraclavicular region and then went after a week. ? diagnosis.

1 *week later*. Maggot expressed by mother from a sore at the middle of the posterior border of the right sternomastoid. There was a small definite hole through which the maggot had been passed, surrounded by inflammatory oedema. The doctor expressed a bead of pus through the small opening.

There was a red inflammatory line 2 in. long and ¼ in. wide passing downwards from the opening.

At the beginning of the illness the child was suffering from facial impetigo.

The boy was camping last summer (1935) in the country and there is a farm quite near his home.

It may be noted that Hope (1840) summarizing the literature to that date had only one case of myiasis by *Hypoderma* sp. to report, and Austen (1912) does not mention *Hypoderma* as causing human myiasis in the British Isles. It is, however, highly probable that cases occur more frequently than records in the literature (e.g. Style (1924)) indicate. Infection by *Hypoderma* is of fairly frequent occurrence in U.S.A. (*vide* Bishopp *et al.* 1926).

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CEPHALOBUS PARASITICUS N.SP. AND "PSEUDO-STRONGYLOIDIASIS" IN *MACACA IRUS MORDAX*

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(With 3 Figures in the Text)

Experience has shown that if the pitfalls of experimental work with some of the parasitic nematodes are to be avoided, helminthologists should possess a sufficient knowledge of the morphological and biological characteristics of the free living nematodes inhabiting water, soil and decomposing organic material as well as the nematodes, parasites or semiparasites of plants. Especially necessary is such information in the study of the biology of *Strongyloides*.

Helminthological literature is replete with instances of the mis-identification of saprophagous nematodes with the free-living generation of *Strongyloides* spp. This error is most easily incurred when resort is made to the cultural method of diagnosing infection. On several occasions workers conducting research on *Strongyloides* have detected such worms contaminating cultures and constituting a fertile source of confusion with the free-living generation of the parasite. Thus, Sandground (1925) found that a large proportion of human *S. stercoralis* infections diagnosed as such in clinical laboratories in the state of Georgia (U.S.A.) were in reality cases of pseudo-parasitism involving a coprophilous nematode *Rhabditis hominis* contaminating the stools after defaecation. Goodey (1927), while studying *Strongyloides ratti*, found that cultures made from rats' faecal pellets may become contaminated with a nematode designated *Cylindrogaster coprophaga*. The most recently described case of "pseudo-strongyloidiasis", is recorded by Chandler (1938), who found *Diploscapter coronata* living in the hypo-hydrochloric stomachs of nine patients in Texas, the worms having initially been identified as *Strongyloides* in a clinical laboratory.

Chandler's cases differ from the others that we have cited in that the nematodes were not simply transients making a "non-stop" tour of the alimentary, but were actually multiplying in the stomach which had apparently been rendered suitable as an environment for residence.

Another instance of true, even though non-pathogenic, parasitism by a species of nematode whose congeners are essentially saprozoites is reported by McIntosh & Chitwood (1934) who found *Longibucca lasiuri* colonizing the stomach and small intestine of two kinds of bats.

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In the present paper I wish to record a further instance of true parasitism by a nematode, which although capable of living independently has been found by us in eleven out of sixteen common monkeys, *Macaca irus mordax* (formerly *M. cynomolgus*) caught in the environs of Batavia.

Examination of the mucosa of the stomach of these monkeys showed this organ to be infested with large numbers (several hundreds) of males, females and various sized larvae of a nematode showing marked differences from *Strongyloides fuelleborni* with which all the monkeys were naturally infested. All the larvae were found to be of the rhabditiform type. Closer examination of the male worms revealed that they differed from the male of *Strongyloides* (Kreis, 1932; Faust, 1933) particularly in the size and shape of the spicules and gubernaculum. The most conspicuous difference between the females and those of the free-living generation of *Strongyloides* was that in the former the vulva is less salient and is located in the posterior third of the body, the uterus being single and as a rule containing fewer eggs which rapidly hatch in uterus.

Cephalobus parasiticus n.sp.

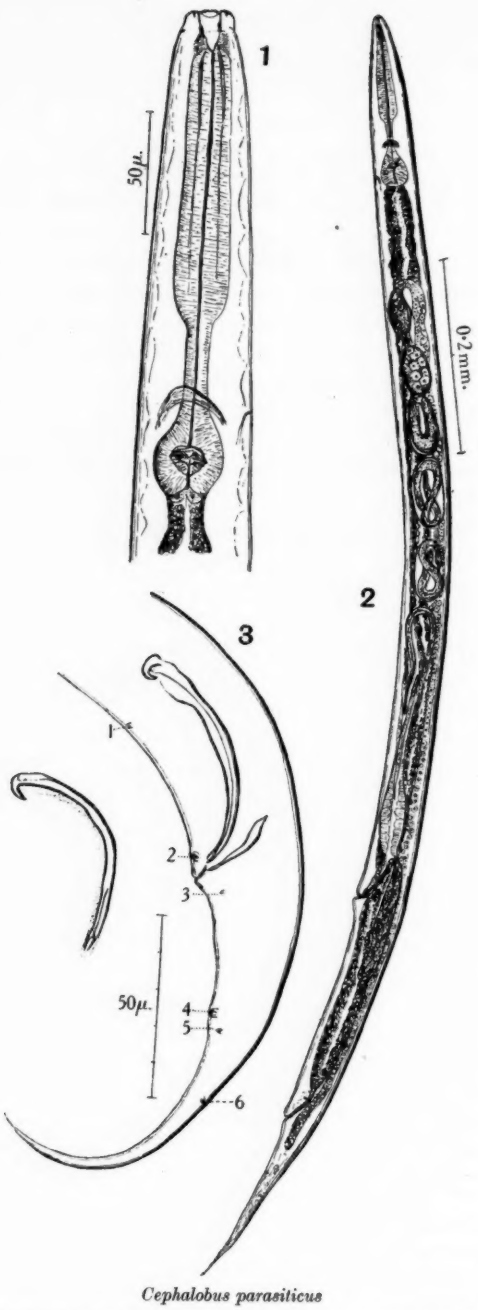
Dimensions.[1] Female: length, 900–1450μ; the greatest width, 35–48μ; length of oesophagus, 162–205μ; vulva to anus, 130–300μ; length of tail, 125–210μ.

Male: length, 780–1120μ; greatest width, 33–40μ; length of oesophagus, 140–190μ; length of tail, 100–150μ; length of spicules, 65–70μ; gubernaculum 25–28μ.

Description. The fully mature worms of both sexes are of the same order of length but are rather more slender and less sluggish in their movement than individuals of the free-living generation of *Strongyloides stercoralis* from man. The cuticle appears to be devoid of striae, but it is really very delicately striated as can be seen under the highest magnifications in favourable preparations. Mouth surrounded by six inconspicuous rounded lips; cephalic papillae barely perceptible, one at the summit of each lip. We were unable, with available equipment, to secure a satisfactory view of the head from the anterior face. There is a very shallow constriction of the body immediately behind the lip region. Lateral fields inconspicuous. In both sexes the tail is drawn out to an acute point and is of moderate length.

Oral vestibule consists of a relatively wide cylindrical chamber, 7μ by about 5μ wide, with thin filamentous walls and conspicuous, though short, refractile cuticular rods (telorhabdions) at the base where the vestibule narrows to form an infundibular part (see Fig. 1). The oesophagus, comparable in all features with the rhabditiform generation of *Strongyloides*,

[1] These measurements were taken from a large series of sexually functioning worms taken from parasitic abode as well as worms propagated for several generations on agar plates. Mature worms, as shown by the above figures, vary considerably in size. As parasites in monkeys they often approach the maximum size of their growth range and the females carry more eggs and larvae in the uterus.



Cephalobus parasiticus

Fig. 1. Oesophageal region. Fig. 2. A young mature female.
Fig. 3. Caudal extremity of male.

consists of a fusiform corpus set off by a well-developed isthmus from the more or less pyriform bulb, which contains a series of finely serrated elements in its central valve. The intestine usually contains dense dark brown granules in its walls and opens by a well-cuticularized rectum to an inconspicuous anus. Nerve ring surrounds the oesophageal isthmus. Excretory tubule and pore exceedingly fine and seen only occasionally after intravitam staining with Nile-blue.

Female. The non-salient vulva is situated in the posterior third of the body not more than 300μ from the anus (Fig. 2). There is a muscular vagina which leads into a well-developed ovejector chamber from the junction of which a caecal appendix, possibly glandular in function and probably a relic of the ancestral posterior genital tube, is given off. This organ reaches midway to the anus and is often obscured by the intestine. In culture the uterus of the young female may contain as few as two developing eggs. More mature females, especially those taken from the parasitic habitat, may contain as many as fifteen eggs arranged in double file *in utero*; many of the older eggs are fully developed. The larvae escape from the egg *in utero* and birth, so far as our observations show, is always viviparous.

At the entrance to the uterus anteriorly there is a receptaculum seminis containing large rounded sperm cells. The oviduct is reflected backwards and the ovary often extends beyond the anus into the tail region. The embryos on hatching measure about 200 by 18μ.

Male. In shape, the tail of the male is similar to that of the female. In the caudal region of the male there are six pairs of minute latero-ventral papillae, two pairs pre-anal and four pairs post-anal as illustrated in Fig. 3. Of these papillae, pairs 2 and 4 are located nearer the mid-ventral line and are more conspicuous than the remainder which are often difficult to demonstrate. The single testis extends to within a short distance of the oesophagus and is always reflected posteriorly. Spicules equal and similar in shape. They are colourless and provided with membranous alae throughout their length. Especially characteristic of the species is the structure of the distal knobbed end of the spicules and their proximal extremities which, when exerted from the cloaca, are seen to be split to produce two (or three?) extremely fine "splinters". The gubernaculum is a narrow acicular structure about 4–5μ wide in its middle and pointed at both ends.

Co-type specimens will be deposited in the British Museum of Natural History and the Helminthological Collection of the U.S. National Museum, Washington, D.C.

SYSTEMATIC RELATIONS

The genus *Cephalobus* Bastian, 1865, is a large one, the majority of whose species live free in the soil or in fresh water. A number of species are saprozoic but, as shown by Marcinowski (1907), some of these have the capacity to parasitize the roots of plants. Because of this capacity to assume the role of

parasitism and because of the morphological resemblance between *Cephalobus* and the free-living generation of *Strongyloides*, we may suspect that phylogenetically the latter was derived from a *Cephalobus*-like ancestry. Furthermore, for several species of *Cephalobus* only females are known and these are capable of propagation without the intervention of a male.

Most of the described species of *Cephalobus* (*sensu lato*) have short rounded tails; others are pointed with spike-like appendages.

From the invaluable monograph of Micoletzky (1921) it appears that only one species of *Cephalobus* has been described from Java, namely, *C. brevicaudatus* Zimmermann, 1898, recorded from the roots of coffee trees. From this species, as well as from others whose description has been available in the East Indies, the species here described differs in many significant morphological criteria. We believe this species to be new and propose for it the name *C. parasiticus*.

Despite the implications of the specific name it is conceivable that this species may also be found leading a non-parasitic existence.

Biology

As previously stated, *Cephalobus parasiticus* was found in the gastro-intestinal tract of eleven out of sixteen young *Macaca irus mordax*, a common monkey in the environs of Batavia, secured for a special study. Few of the monkeys of the same species in the stock colony of the Pathological Institute appear to harbour this nematode, but no difficulty was experienced in infesting a test animal by administering adult worms and larvae through a gastric sound.

Often the worms are present in the fundus of the stomach in extremely large numbers but they are to be found also, albeit in lesser numbers, throughout the remainder of the alimentary tract, from duodenum to colon. Although they congregate especially in contact with the walls of the stomach, sections of the stomach show the mucosa to be intact. We find therefore no evidence that the worms can penetrate into tissue despite the active boring movements that are exhibited by larvae and adults alike.

Because of this boring movement, resembling that of the filariform larvae of *Strongyloides*, an attempt was made to infect three human volunteers by placing some fifty or more larvae and adults on the skin on the under side of the forearm. No irritation of the skin, such as is produced by larval penetration, followed the drying of the water which contained the worms and subsequent culturing of the faeces has failed to reveal an infection.

Attempts were also made to infect four young albino rats, and a guinea pig by delivering large numbers of worms (adults and larvae) to the stomach via a rubber catheter. These animals were killed from 2 to 5 days after feeding and the entire alimentary tract was carefully examined under a dissecting microscope. The results were uniformly negative. It consequently appears that

Cephalobus parasiticus exhibits a high degree of host specificity, or its colonization of animals depends on peculiar circumstances. However, the parasite was found to be relatively easily cultured *in vitro* on bouillon-agar plates in Petri dishes at laboratory temperature (*ca.* 26–31° C.).

The cultures do not fare so well when maintained in the 37° C. incubator or when the substratum is blood agar. This seems to be due to the over-abundant growth of certain bacteria inimical to the nematodes.

At room temperature on bouillon agar the worms multiply prolifically although they seldom attain the same size as they do in the stomach of the monkey. By transplanting occasionally to fresh medium *C. parasiticus* has been propagated *in vitro* for two months at the time of writing. The worms therefore may be regarded as saprozoic and facultatively parasitic in monkeys.

SUMMARY

Cephalobus parasiticus is described from eleven out of sixteen young specimens of *Macacus irus mordax* (synonym, *M. cynomolgus*) caught in the vicinity of Batavia.

The species, which strikingly resembles and is easily capable of being confused with the rhabditiform free-living generation of *Strongyloides*, is found in the stomach and intestine of the monkeys but is apparently non-pathogenic. This nematode appears to be unable to establish itself in the rat and guinea-pig but is capable of being propagated indefinitely on bouillon agar at room temperature.

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THE COMMON FLAGELLATE OF THE HUMAN MOUTH, *TRICHOMONAS TENAX* (O.F.M.): ITS DISCOVERY AND ITS NOMENCLATURE

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(With 1 Figure in the Text)

Uncertainty and disagreement still exist among protozoologists regarding the proper name of the trichomonad flagellate which is commonly found in the human mouth and generally called "*Trichomonas buccalis*". The nomenclature of this organism undoubtedly presents several awkward problems; but I believe all of them can be solved simply and satisfactorily if we merely read aright the description recorded by its discoverer, and consequently recognize the validity of his original specific name.

For many years I have been persuaded by the evidence available (1) that the *Trichomonas* of the human mouth is specifically distinct[1] from the similar forms found in the intestine and genito-urinary system of Man (*T. hominis*, *T. vaginalis*); and (2) that it was discovered and first described by the old Danish naturalist Otto Friderich Müller (1730–1784)—one of the most venerable Fathers of Protozoology. The first point I need not discuss here, as it is a conclusion now widely accepted: the second is that to which I would particularly direct the reader's attention. If this inference also be allowed, then the nomenclature of the organism in question can probably be determined for all time. That such a result is highly desirable nobody will dispute.

I propose to say nothing here—though I could say much—about the cryptic references to "*Trichomonas buccalis*" in the writings of Ehrenberg, Bory de St.-Vincent, Mandl, and other early workers: for these authors did not know the organisms actually concerned, nor did they appreciate our present problems. I shall also now avoid all discussion of modern records of *Trichomonas* from the mouths of mammals other than Man: for consideration of these would take us too far afield, and could lead to no helpful conclusions at the present moment.

I now invite the reader to consider—or reconsider—the account of "*Cercaria*

[1] I have previously referred to this organism twice in print (Dobell & O'Connor (1921), p. 70 note: Dobell (1934), p. 556 note)—on each occasion to emphasize that I regard it as a distinct species. Despite these clear statements, Westphal (1936) and some other recent writers now allege that I suppose *all* the trichomonads of Man to be specifically identical. This is untrue, and I therefore note the fact in order to avoid misunderstanding by readers who have not consulted my previous writings.

tenax" published by O. F. Müller in 1773, 1776, and 1786.[1] On pp. 69–70 (Vol. I, part 1) of the *Vermium terrestrium et fluviatilium...succincta historia* (1773) the following record will be found:

62. CERCARIA TENAX.

CERCARIA membranacea, antice crassiuscula truncata, cauda triplo breviore.

Dan. SEI-HALEREN.

M. *Lende* aliquantum major.

Membrana obovata pellucida, margine antico crasso, truncato; postice acuta seu in caudam brevissimam terminata.

Interanea nulla.

Celeri gyro in varias directiones vagatur. Striae licet, quae evaporatione aquae formantur, jam appareant, quantillum [p. 70] tamen humoris residuum natationi strias & sulcos absque impedimento sensibili pervagantis horae semiquadrante sufficit.

In infusione sordium dentium intra quatriduum.

This description was repeated in 1786 (pp. 136–7) with trifling variation of detail[2] but the very important addition of illustrations[3] (with brief description). I therefore reproduce these here ($\times 2\frac{1}{2}$ diameters, as the originals are very small) with the original explanation.

Between 1773 and 1786 Müller published (1776) his "*Prodromus*", or preliminary survey, of the fauna of Denmark and Norway. In this, *C. tenax* is listed under "VERMES, Infusoria", with the very brief definition as above,[4] and no illustrations. This catalogue-entry obviously needs no further notice.

[*Tab. XX*] Fig. 1. *Cercariae Tenacis*, quatuor exempla, aucta magnitudine, exhibent.
a. pars antica crassior.
b. caudula.

Let us now consider in detail what Müller tells us about the structure, size, habitat, and movements of his "*C. tenax*". I may preface my remarks with a reminder that our author was not only a naturalist but at one time also a private tutor and teacher of languages. Everyone who has carefully studied his works knows that he was not merely an accurate observer—though handi-

[1] Müller died on 26 Dec. 1784, and the illustrated edition of his work was published posthumously under the title *Animalcula Infusoria* [etc.] by his widow, Anna, who got the Danish zoologist and Greenland missionary Otto Fabricius (1744–1822) to edit it. Anna Müller (1735–1787) was daughter of Bishop Rasmus Paludan, and had been married previously to a merchant (Christen Carlsen). She died the year after the publication of *Anim. Infus.* (1786)—for which she probably paid, as she possessed considerable private means. O. F. M. himself was a poor man.

[2] The differences are: species numbered 141 (instead of 62); references to plate and figures added; reference given to previous publications; Danish name omitted; "*Mon. Lende*" substituted for "M. *Lende*"; "*Interanea*" not italicized.

[3] Fabricius tells us in his preface that the pictures in *Anim. Infus.* were all faithfully drawn from life, and also engraved, by Müller's own brother, who was an accomplished artist.

[4] "2487. *C. Tenax* membranacea, antice crassiuscula, truncata, cauda triplo breviore. *Sei-Haleren.*" Nothing else is recorded.

capped, of course, by the limited microscopic resources at his command—but also a good Latin scholar. He evidently took great pains to observe things correctly and also to record his observations exactly in correct and even elegant language. We should therefore do him an injustice if we were to dismiss his words lightly, without attending to those finer details to which he himself devoted so much care.

First, it should be noted that Müller (1773) subdivided the species of his genus *Cercaria* into two groups—*teretes* and *depressae*, the rounded and the flattened:[1] and he placed *C. tenax* in the latter subdivision. (This may explain also why he called it "*membranacea*".) From his description as a whole it appears that the organism was oval but flattened; plumper, and truncated, anteriorly; highly transparent; and furnished at the narrower hinder end with a sharply pointed little tail, about one third as long as the body. No internal organs were visible. The minute figures (1786) agree well with this description, but indicate no flattening.

As regards the size of the organism we learn only—since Müller could record no accurate micrometric measurements—that it was "considerably[2] larger" (*aliquantum major*) than "*Monas lens*". What this name itself denotes is with difficulty deducible from Müller's own words, and it has been interpreted in various ways by subsequent writers. But it was a name which he bestowed (*inter alia*) upon certain micro-organisms discovered in the human mouth by Leeuwenhoek in 1683, as his references (1773, p. 26) prove: and Müller identified Leeuwenhoek's organisms—not unreasonably at that date—with similar forms discovered by other early micrographers in various organic infusions. I have discussed Leeuwenhoek's buccal micro-organisms in detail elsewhere,[3] and have shown that they were all various well-known forms of bacteria. It may reasonably be assumed, therefore, that *C. tenax* was an "animalcule" definitely larger than the bacteria which live in the same environment.

Mention of the environment leads to the consideration of what Müller recorded about the habitat of *C. tenax*. His words are brief, and admit of more than one interpretation: "in an infusion of dental scum inside a period of four days". It is obviously not justifiable to translate "*sordes dentium*" as "tartar", or to assume that Müller made a culture from this and found *C. tenax* developing in it four days later. Such conceptions[4] are foreign to the text, and can be dismissed at once as anachronisms. From Müller's own description and

[1] The subheadings "*teretes*" and "*depressae*" (1773, pp. 64, 68) were omitted from the version of 1786; but they are there replaced by the statement (p. 119, footnote 12) that "*Cercariae possunt subdividi in teretes... & depressas.*"

[2] A classical meaning of *aliquantum* is "more than a little", though it may also signify "somewhat", or "a little" (*aliquantulum*). See the great Dictionary of Facciolati & Forcellini.

[3] Dobell (1932), p. 236 *seq.*

[4] Cf. Kofoid (1920), Wenyon (1926). "Tartar", in its modern dental sense, was apparently unknown to Blankaart and other medical lexicographers of the eighteenth century. According to the *Oxford English Dictionary* the word was first used in English with its present connotation in 1806. "Cultures" are, of course, even more recent—so recent, indeed, that they were first mentioned, according to the same authority, in 1884.

references we can, however, conclude legitimately that he had read Leeuwenhoek's account of the bacteria found in the *materia alba* on and between human teeth; and that in this material—mixed with water, in repetition of Leeuwenhoek's procedure—he himself discovered larger and undescribed "animalcules" (*C. tenax*) which persisted in his preparations for not more than four days.

Müller's names for his organisms—both "Latin" and "Danish"—may be noted at this point. As everyone knows, his genus *Cercaria* included a very heterogeneous assortment of creatures, but its definition and status need not now detain us. The "genus" is now of more interest to helminthologists than to protozoologists. The derivation of the Latin name is obviously from the Greek κέρκος [=tail], and explains the Danish equivalent (*Haleren*, from *Hale* [=tail]) which Müller likewise invented. *Sei* (=*sej* or *sejg*) means "tough" or "tenacious", and is thus an exact translation of *tenax*. We might render "*Haleren*" as "tailer" in English—were it not for the sartorial suggestion—and "*Sei-Haleren*" accordingly as "the tough tailer": but my Danish friend Dr S. N. Vendel (Copenhagen)—whose knowledge of English is first-rate—tells me that the terms are really untranslatable into our language (and even difficult to understand in his). It is tempting to suppose that Müller called his animalcule *sei* (*tenax*) because it could survive so long as four days outside its natural habitat in the mouth.[1]

The rest of Müller's description of his "animalcule" seems to me unambiguous and well expressed, though it has apparently been misunderstood by more than one later interpreter. I read his words ("*Celeri gyro...sufficit*") approximately thus in English: "It wanders hither and thither with rapid rotation. And although streaks, formed by the evaporation of the water, soon make their appearance, yet what little moisture remains among these streaks and the intervening furrows is enough for it to swim about in, without any obvious hindrance, for a half-quarter of an hour." It is clear that the "streaks" (*striae*) mentioned in this passage were deposits formed by the drying up of the liquid, and not preformed elements (such as *Leptothrix* filaments). No such meaning can be read into Müller's words, though at least one commentator appears to have taken this view.

If we attend carefully to what Müller wrote, and examine his illustrations with due allowance for his difficulties, it seems to me that we can draw only one conclusion from them: he saw, and attempted to describe, the now well-known *Trichomonas* of the human mouth. This organism has the form, size, and appearance which he indicated—save only that it is not "flattened" or "membranaceous" (an error of observation very easily made even now, with a good microscope).[2] It occurs in the "dirt on teeth" fairly commonly, and

[1] But Müller gave the same specific name to another animalcule also (*Proteus tenax*; 1786, p. 10), which I believe to have been the Euglenoid *Peranema*. In this case the epithet appears to have been suggested by the viscosity of its "gelatinous" protoplasm.

[2] I believe that Müller was led to this view partly by erroneous comparison of "*C. tenax*" with the Euglenoid *Phacus*, to which *Trichomonas* bears a superficial resemblance under inadequate magnification. Cf. his figures of "*Cercaria pleuronectes*" (1786; Pl. XX, figs. 19–21).

can survive outside the mouth, at ordinary room-temperatures (under otherwise favourable conditions), for several days. The movements described are characteristic, and can apply only to a flagellate or a ciliate: and it is now certain that no ciliate protozoon normally inhabits the human mouth. If the flagella and undulating membranes—which he was unable to discern with his primitive glasses[1]—were added to Müller's figures, they would be readily recognizable at the present day.

Accordingly, it seems to me certain that "*Cercaria tenax*" was the *Trichomonas* of the human mouth. The original description contains a sufficient "indication" of its characters, as required by the International Code of Nomenclature, to justify the maintenance of the specific name. At all events, the indication is no less certain than that for dozens of other Müllerian genera and species which are nowadays accepted universally.

So far as I am aware, only two recent writers on the trichomonad of the human mouth have considered Müller's claim to its discovery and the validity of his specific name.[2] Both of them have dismissed his case—without adequate reason, as it seems to me—so I must now briefly note their arguments and conclusions.

(1) Kofoid (1920, p. 157) begins by saying that "The discoverer of the flagellate of the mouth was O. F. Müller,...who ransacked a culture made from the tartar[3] between dirty human teeth and found therein (1773, 1776) and figured (1786) tiny organisms which he included in his genus *Cercaria* as *C. tenax*." Although Kofoid thus spoke of "*the* flagellate"—not "*a* flagellate"—and made this very definite statement, after some discussion he "rejected" (his own word) the specific name *tenax* because "Müller's figures are so imperfect and his description so meagre". He then admits that "only one flagellate from the human mouth has thus far been definitely identified in the course of modern investigation of the microfauna of that habitat", but considers "It may well be that with additional investigation more than one kind of flagellate will be found in the mouth."

Since these words were written another flagellate has, indeed, been recorded from the human mouth. This is a species of *Bodo*, described by Knowles and Das Gupta (1924). How this typically free-living organism gained access to the mouth in question is enigmatic, yet it is tolerably certain that no species of this genus normally lives in the mouth of Man. *Trichomonas* is still the only known flagellate commonly occurring in this situation. But even if—as seems highly improbable—other flagellates should, eventually, be proved to live there, this does not automatically rule out the name *tenax*. If we agree that Müller applied this to *a* flagellate—as Kofoid clearly admits—then it would

[1] Müller—like Leeuwenhoek—preferred simple lenses to the compound microscopes of his period, which, though they gave a greater magnification, gave less distinct images. He generally employed lenses of English make, and never used a "solar" microscope. Cf. Müller (1773), p. 16.

[2] Among the older authors Moquin-Tandon (1860) alone appears to have recognized Müller's specific name, but he erroneously referred the organism to Bory's genus *Virgulina*.

[3] Cf. p. 140 *supra*. The "tartar" and "culture" are unwarranted additions to the original text.

be more conformable with custom and the International Rules to assign it to *one* of the oral forms rather than to reject the name entirely.

It should be added that Kofoid (1920) considers[1] that the correct name of the trichomonad of the human mouth is *Trichomonas buccalis* Goodey & Wellings, 1917. But this name was proposed by Goodey alone (not Goodey *and Wellings*[2]), and there are several other names—disregarded by Kofoid—which have undoubted priority over *buccalis*. Kofoid's rejection of the name *tenax* seems all the more illogical when we read in two of his later papers[3] that "O. F. Müller in 1773 described a pear-shaped organism occurring in the human mouth[4] to which he gave the name *Cercaria tenax*. . . . Since no organism other than *Trichomonas buccalis* occurs in the human mouth which even remotely resembles a cercaria, it is probable that Müller . . . was first to record this infection." I agree with this statement in general, and can only wonder why Kofoid failed to draw the obvious nomenclatural conclusion.

(2) The second recent author who has discussed the discovery and nomenclature of "*T. buccalis*" is Wenyon, whose very different conclusions must now be considered.

Wenyon (1926; **1**, 656) briefly records the earliest observations on "*T. buccalis*" in the following words: "It is probable that Leeuwenhoek [no reference given] saw the flagellate in the tartar of his own and other people's teeth. . . . Müller (1773) also noted that flagellates developed in the course of four days in water to which tartar from the teeth had been added. He named the organism *Cercaria tenax*, but there is no conclusive evidence that he was actually dealing with *Trichomonas*." But there is no evidence at all that Leeuwenhoek ever saw flagellates in the human mouth, as I have shown elsewhere:[5] and, as I have just noted above, there is "no conclusive evidence" in Müller's words to prove that his *C. tenax* "developed" in water to which "tartar" had been added. He never said so.

In Wenyon's opinion the correct name of the trichomonad of the human mouth is neither *T. tenax* (O. F. M.) nor *T. buccalis* Goodey, but *Trichomonas elongata* Steinberg, 1862. He writes: "Steinberg (1862) studied these oral flagellates and named three distinct species: *T. elongata*, *T. caudata*, and *T. flagellata*. It is evident that he was dealing with various forms of one flagellate, so that if the oral *Trichomonas* be regarded as a species distinct from that of the intestine, its proper name will be *T. elongata*, the first of those proposed by Steinberg." Although the work of this author is only indirectly connected with the present discussion, I must devote a few words to it here.

[1] Cf. also Kofoid (1929) and Kofoid, Hinshaw, & Johnstone (1929).

[2] These words are thus italicized by Kofoid (1920, p. 156), as though to emphasize the error. As stated above, the name *buccalis* was proposed by Goodey, in a note appended to a joint paper with Wellings—not by both authors.

[3] Kofoid (1929), p. 167; Kofoid, Hinshaw, & Johnstone (1929), pp. 15–16 [reprint]. The same words occur in both papers.

[4] This is an obvious exaggeration of Müller's words; but *if true* it would greatly strengthen my case and weaken Kofoid's.

[5] Dobell (1932), p. 236 *et seqq.*

The paper by Steinberg (1862) was published in a Russian medical journal which I have been unable to find in England. But my friend Dr C. A. Hoare —hearing of my fruitless search—obtained an accurate transcript of it from Prof. E. N. Pavlovsky (Leningrad) in 1922, and then very kindly supplied me with a complete English translation. I am therefore acquainted with its contents, and so cannot ignore this publication—as Kofoid evidently does[1]—for the reason that it "is in an inaccessible journal in the Russian language."

Steinberg's paper is interesting, but all his findings cannot now be accepted as accurate. In the *materia alba* from human teeth (chiefly his own) he identified and described—besides various bacteria—no less than 15 species of protozoa, which comprised *Monas* (4 species), *Bodo* (2 spp.), *Cercomonas* (3 spp.), *Trichomonas* (5 spp.), and *Amoeba* (1 sp.). The 5 species of *Trichomonas* were, with the other forms, first tabulated (p. 378) and afterwards described in order. The order, in the table, is (1) *T. vaginalis*, (2) *T. crassicauda*, (3) *T. elongata*, (4) *T. caudata*, (5) *T. biflagellata*. In the ensuing text these organisms are described in the following sequence: (1) *T. vaginalis* (p. 455); (2) *T. biflagellata* (p. 455); (3) *T. caudata* (p. 456); (4) *T. elongata* (p. 456); (5) *T. crassicauda* (p. 456). The species "*T. flagellata*", mentioned by Wenyon, does not occur at all in Steinberg's paper.

If we exclude "*T. vaginalis*", for obvious reasons, it follows that Steinberg's first name for the *Trichomonas* of the mouth was *T. crassicauda* (table, p. 378) or *T. biflagellata* (text, p. 455). *T. elongata* clearly has no claim to preference on grounds of page-priority, and I am thus at a loss to understand why Wenyon selected it. A possible explanation, however, may be that he merely paid undue tribute to a literary tradition; for his string of names is by no means original. The earliest reference which I have seen to Steinberg's work is the well-known passage in Leuckart (1879), who—without consulting the original —records his "species" as "*Trichomonas elongata*, *Tr. caudata*, and *Tr. flagellata*." Later, Brass (1884, p. 15) notices unfavourably Steinberg's "3 so-called species from the mouth"—"T. elongata, caudata, and flagellata." Blanchard, soon afterwards (1885; **1**, 88), repeats that the Russian author reported "3 flagellates" from the human mouth—"*Trichomonas elongata*, *Tr. caudata*, and *Tr. flagellata*"; while Braun (1895, p. 114) and Doflein (1909, p. 418*n*) reiterate the very same names and sequence. It is at least a curious series of coincidences that Leuckart, Brass, Blanchard, Braun, Doflein, and Wenyon all say that Steinberg described three species (not five, as he actually did); that they all give the same three names in the same order (which is not found in the original Russian version); that they all mention "*T. flagellata*" (not in Steinberg); and that they all ignore *T. biflagellata* and *T. crassicauda* —either of which might clearly claim priority over the other three.

Nevertheless, I agree with Wenyon that all Steinberg's "species" of

[1] Kofoid (1929), p. 167. It is singular that this author, in this article, notices (giving a reference to the original) and condemns (p. 154) Steinberg's observations on *Entamoeba gingivalis*. These were recorded in the very same "inaccessible" paper.

Trichomonas probably denoted only one actual species of flagellate. But I reject all five of his specific names—and also the mythical "*T. flagellata*"—because they appear to be but synonyms of *Cercaria tenax*, which was discovered, described, figured, and orthodoxly named by O. F. Müller more than three-quarters of a century earlier.

It is now generally recognized that only one flagellate normally lives in the mouth of Man, and that it is correctly assigned to the genus *Trichomonas* Donné. The chief synonyms of this genus I have noted elsewhere,[1] but I must add here that Donné's name dates from 1836—not 1837, as usually supposed: for his well-known memoir (1837) on "the nature of mucuses", containing the classical description of *T. vaginalis*, was preceded by an earlier note (1836) which has been generally overlooked. In this the irregularly formed but now —in amended form—universally accepted designation "*Trico-monas vaginale*" was first published.

T. vaginalis Donné is the type of *Trichomonas*, and to this genus the common flagellate of the human mouth undoubtedly belongs. If, as seems at present probable, this species is distinct from that found in other parts of the human body;[2] and if, as I believe, it was discovered and named originally by O. F. Müller: then its nomenclature and synonymy may be briefly indicated in conclusion. The following list of names bestowed on the flagellate of the human mouth crystallizes the facts and arguments advanced in the foregoing pages:

Trichomonas tenax (O. F. Müller, 1773)

Syn. *Cercaria tenax* O.F.M., 1773 (1776, 1786)
Virgulina tenax (O.F.M.) Moquin-Tandon, 1860
Trichomonas vaginalis Steinberg, 1862 [*nec* Donné, 1836]
Trichomonas crassicauda, *Trichomonas elongata*, *Trichomonas caudata*, *Trichomonas biflagellata* } Steinberg, 1862
Trichomonas flagellata Leuckart, 1879; Brass, 1884; Blanchard, 1885; Braun, 1895; Doflein, 1909; Wenyon, 1926 [*non* Steinberg, 1862]
Cercomonas intestinalis Rappin, 1881 [nec *C. intest.* auctt. var. al.]
Trichomonas hominis Prowazek, 1902[3] [*nec* Davaine, 1860]
Tetratrichomonas buccalis Goodey, 1917
Trichomonas elongata (Steinberg) Wenyon, 1926
Trichomonas buccalis auctt. var. passim

[1] Cf. Dobell, in Dobell & O'Connor (1921), p. 86.

[2] Calkins (1933), p. 361, has recently added to the humour and complexity of the subject by stating that Wenyon himself recorded *Trichomonas* from the "toe-nails". This is apparently a misreading or misprint of "tonsillitis" (Wenyon, 1920) or "tonsil" (Wenyon, 1926) in the English author's accounts of the trichomonad of the human mouth.

[3] Prowazek (1902) identified the flagellate of the mouth as *T. hominis* Davaine, but stated that he regarded it as a subspecies (for which he proposed no name). Other writers (*e.g.* Rappin, 1881) have also referred the organism to the same species or its synonyms (*T. intestinalis* Leuckart, etc.). For the synonymy of *T. hominis* see Dobell, in Dobell & O'Connor (1921), p. 65.

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